The effects of the macroalga *Gracilaria gracilis* and increasing temperatures on the performance of the endemic Cape eelgrass *Zostera capensis*

BY

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Plagiarism Declaration

I know the meaning of plagiarism and declare that all of the work in the dissertation, save for that which is properly acknowledged, is my own.

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Abstract

Rising temperature caused by global warming alters physiology, phenology and/or distribution in a wide array of plant and animal species, which has dramatic knock-on effects at different levels of organisation. This study investigates the individual and interactive effects of temperature (18°C, 22°C and 30°C) and additions of the macroalga *Gracilaria gracilis* (high and low) on the performance of the seagrass *Zostera capensis*, which occurs in Langebaan Lagoon, South Africa over a seven-week period. Results from the laboratory experiment revealed that *G. gracilis* did not significantly affect the performance of *Z. capensis* although temperature did result in greater leaf width, fouling and senescent biomass, as well as marginally greater leaf area and lower below-ground biomass at 30°C. Increasing temperature also increased *G. gracilis* biomass, percent cover and fouling by microalgae. In addition, there was no interaction between temperature and the additions of *Gracilaria*. The overall findings of this study indicate that *Z. capensis* abundance is likely to decrease while *G. gracilis* will conversely increase in abundance in response to warming. Changes in abundance of those two ecosystem engineers highlight the possibility of a phase shift from a seagrass- to macroalgal-dominated state in Langebaan Lagoon.

Keywords: global warming, *Zostera capensis*, *Gracilaria gracilis*, ecosystem engineers, biotic interactions, ecosystem functioning

Introduction

Global climate change

Globally, habitat loss and fragmentation, overexploitation, species introductions and chains of extinction, which are all attributable to human activities, represent the leading causes of extinction (Auld & Keith, 2009; Brooks et al., 2002; LoGiudice, 2006; Purvis et al., 2000; Wilcove et al., 1998). Exacerbating the effects of this 'Evil Quartet', described by Diamond (1989), are emerging infectious diseases and anthropogenically-induced climate change (Ranta et al., 1998; Root et al., 2003; Smith et al., 2006; Thomas et al., 2004). Indeed, the Intergovernmental Panel on Climate Change (IPCC) declared with high confidence that climate change was responsible for more than 95% of the observed changes in biological systems (Parmesan & Yohe, 2003). Unsurprisingly, the literature on the impacts of climate change has grown significantly since the 1990s, with the effects of temperature at the organismal-level and in marine ecosystems being the most-researched topic (Harley et al., 2006). This finding may seem intuitive because even though the recent climatic trends only make up a fraction of the magnitude of changes predicted over the next centuries, they have already generated substantial responses in both plant and animal species, which could have extensive consequences for human welfare and health (Harley et al., 2006; IPCC, 2014).

Human-induced climate change is mediated mainly by deforestation and the combustion of fossil fuel (Chapin III et al., 2000; Harley et al., 2006). Direct consequences include the increase in greenhouse gas emissions such as carbon dioxide and methane in the atmosphere and result in the most rapid climate change ever experienced since the last glaciation period (Chapin III et al., 2000). Changes linked to climate change are sea level rise, changes in ocean circulation, elevated CO_2 accompanied by reductions in pH, as well as

ozone depletion leading to an increase in ultraviolet radiation, and global warming (Austin et al., 1992; Bischof et al., 1998; Connolly & Roughgarden, 1999; Harley et al., 2006; Knowlton, 2001; Pörtner et al., 2005; Svensson et al., 2005). In terms of temperature, current IPCC climate change projections indicate an increase in average sea surface temperatures of 1.0-3.7℃ by 2081-2100 (Fig. 1) and a rise of 0.11℃ per decade has already been observed between 1971 and 2010 in the upper 75 m (IPCC, 2014). It is relatively well-established that temperature affects all biological processes and structures (Shaver et al., 2000; Somero, 2002), and the subsequent impacts of rising temperature have already been documented in numerous plant and animal species (Root et al., 2003). Undoubtedly, global warming is expected to cause dramatic changes in biodiversity but also an unprecedented loss of species (Chapin III et al., 2000; Lovejoy & Hannah, 2006). Generally, species diversity is of central importance since the relative abundance and presence of certain organisms dictate particular traits present, which affect ecosystem functioning and local resistance and resilience (Chapin III et al., 2000; Grime, 1997; Jueterbock et al., 2013; Kordas et al., 2011; McCann, 2000; Worm et al., 2006) (Fig. 2).

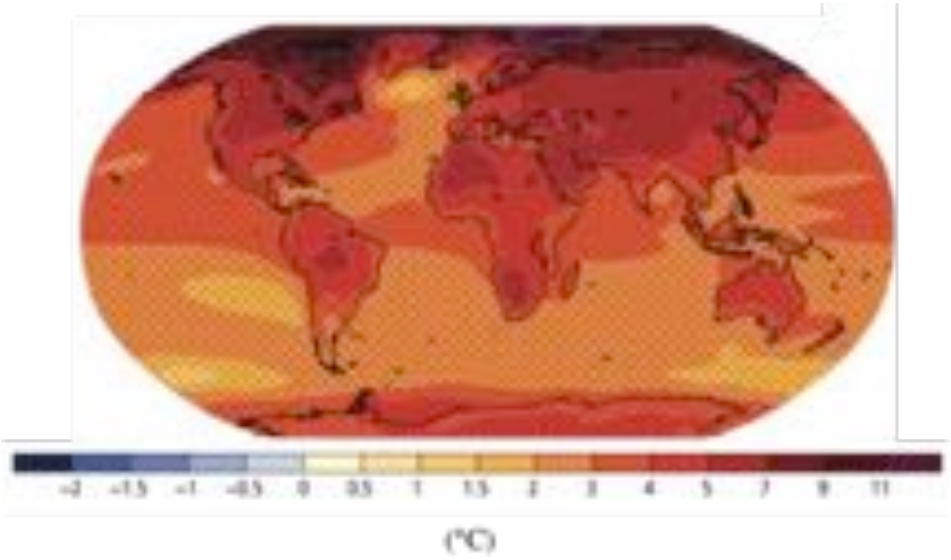

Figure 1: Predicted surface temperature changes for the 2081-2100 period under the RCP8.5 scenarios and relative to the 1986-2005 period (IPCC, 2014).

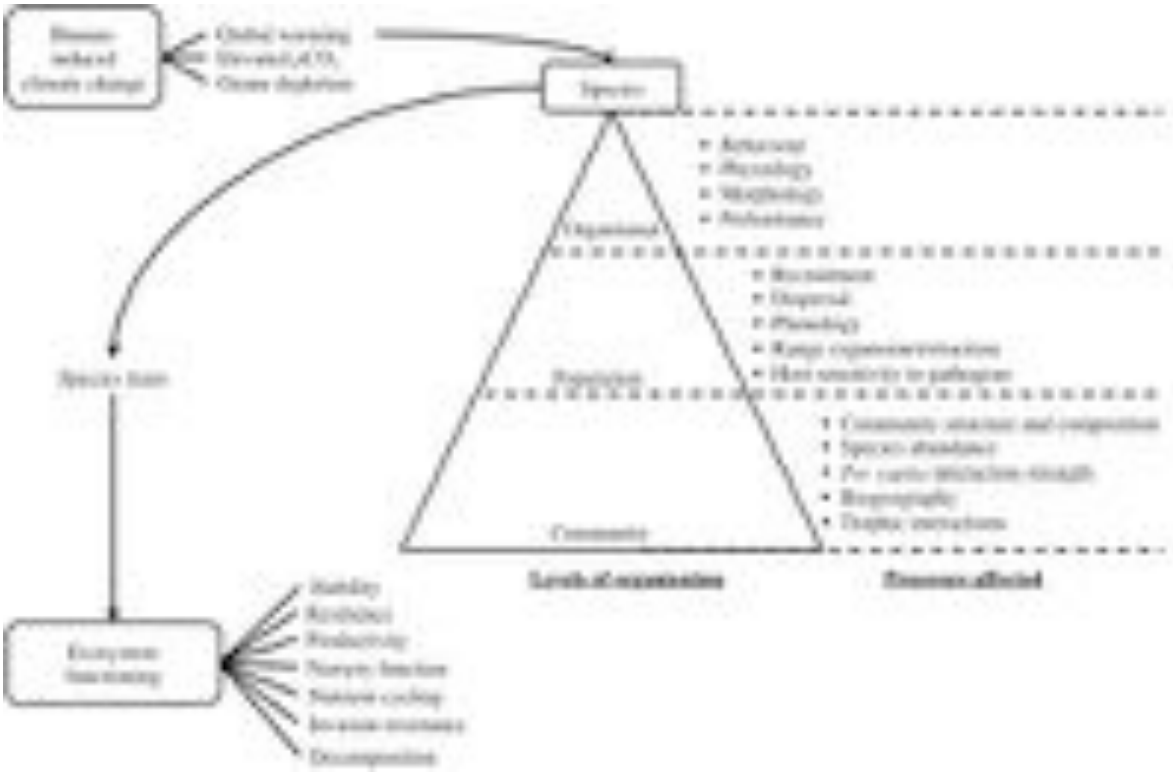

Figure 2: Human-induced climate change is responsible for ozone depletion, increased CO_2 concentrations and global warming. Increased temperature has idiosyncratic effects on species, which has cascading ramifications for higher levels of organisation and broader ecosystem functioning.

Increasing temperature directly impacts the performance of organisms at different stages in their life history cycle through alterations in behaviour, physiology and morphology (Harley et al., 2006; Pörtner et al., 2005). Warmer temperatures typically increase biochemical reaction rates (both catabolism and anabolism), which utilise energy to allow for growth, development, activity and reproduction (Gillooly et al., 2001; Hughes, 2000; Lafferty, 2009; Menge et al., 2008). However, in order to maintain a positive energy balance, food consumption rates have to increase as well, leading to a potential decrease in survivorship (Lafferty, 2009). This is a concern, particularly for non-feeding stages exhibited by some larvae, cysts and eggs, as prolonged exposure to warmer temperatures will likely increase metabolism that drains energy reserves (Fayer et al., 1998; King & Monis, 2007). In plant species, growth, respiration, photosynthesis and tissue composition are likely to be altered by rising temperatures (Cannell et al., 1998; Hughes, 2000; Myneni et al., 1997). Nonetheless, organisms can display a number of mechanisms that help them endure varying temperatures. Examples include heat shock proteins, which allow other proteins to maintain their shape across an array of temperatures, or behavioural thermoregulation used by ectotherms (Bradshaw & Holzapfel, 2001; Feder & Hofmann, 1999; Lafferty, 2009). Species can also acclimatise to rising temperature and ultimately adapt to such conditions (de Jong & Brakefield, 1998; Rodríguez-Trelles & Rodríguez, 1998). However, the ensuing changes associated with adapting systems and repairing thermal damage through the restructuration of cellular membranes or the activation and operation of heat-shock responses for instance, may become costly in terms of energy budgets as it is often achieved at the expense of growth and reproduction (Clarke, 2003; Somero, 2002; Wernberg et al., 2011). As a result, the strength of warming-induced impacts varies among and within species, depending on physiological temperature limits and physiological plasticity (Hampe & Petit, 2005; Harley et al., 2006; Hughes et al., 2003; Somero, 2002; Tomanek & Somero, 1999).

At the population-level, transport processes that influence recruitment and dispersal can be affected by global warming (Harley et al., 2006; Lubchenco et al., 1991; Root et al., 2003). Moreover, shifts in abundances, zonation patterns and biogeographical ranges have been observed over the last couple of decades in a number of organisms in response to rising temperature (Fields et al., 1993; Harley et al., 2006; Keister et al., 2005; Lafferty, 2009; Loarie et al., 2009; Parmesan & Yohe, 2003; Perry et al., 2005; Precht & Aronson, 2004; Somero, 2002; Thomas et al., 2004). This patterning often reflects discontinuities or gradients in temperature (Somero, 2002) and it is estimated that range limits have shifted about 6.1 km northward or metres upward in elevation, per decade (Parmesan & Yohe, 2003), with a maximum shift of 1000 km observed in marine copepods over the last 40 years (Sagarin et al., 1999). As rising temperatures displace thermal habitats, multiple species have shifted their distributions; this concept is also known as niche tracking (Bruge et al., 2016; Monahan & Tingley, 2012) and examples include the Californian neogastropod *Kelletia kelletii*, which exhibited a northward expansion (Precht & Aronson, 2004; Zacherl et al., 2003), the ocean quahog *Arctica islandica*, which displayed offshore and northward range contraction along the Atlantic coast of the United States of America (Weinberg et al., 2002), as well as North Atlantic fishes and sessile intertidal organisms, which have upper vertical limits that are inversely correlated with temperature (Mathieson et al., 1998; Perry et al., 2005). In marine ecosystems, changes in distributions can alter recruitment, food webs and have dramatic consequences for fisheries (Beaugrand et al., 2003; Bruge et al., 2016; Gamito et al., 2015).

There is also a growing body of evidence suggesting that widespread phenological shifts are occurring in response to warming. Studies suggest that spring has arrived about 2.3 days earlier per decade (Parmesan & Yohe, 2003). This phenomenon has led to earlier arrival of migratory birds and butterflies (Ahas, 1999; Bradley et al., 1999; Roy & Sparks, 2000),

tree flowering time (Ahas, 1999; Menzel, 2000) and burdburst (Menzel, 2000; Menzel et al., 2001), bird nesting and hatching (Crick et al., 1997; Crick & Sparks, 1999), and frog breeding (Beebee, 2009).

At the community-level, shifts in thermal niches, which are a response of changes in physiology, phenology and/or distribution, have the potential to disrupt species interactions, directly or indirectly, by altering species diversity and community composition (Beebee, 2009; Both & Visser, 2001; Chapin III et al., 1997; Chapin III et al., 2000; Edwards & Richardson, 2004; Harley et al., 2006; Kordas et al., 2011; Root et al., 2003; Sanford, 1999; Schiel et al., 2004). Alterations in species interactions can modify ecosystem processes or change the relative abundance of species with essential traits (Chapin III et al., 2000; Power et al., 1996). It is generally well recognised that species loss can have deleterious effects on ecosystem stability and has further social and ecological consequences (Grime, 1997; Jueterbock et al., 2013; Kordas et al., 2011; McCann, 2000; Worm et al., 2006). Greater diversity enhances stability in ecosystem functions, thereby conferring greater resistance or resilience against disturbances because of the variety of functional traits, life strategies and responses to environmental disturbances (Downing & Leibold, 2010; Rossi et al., 2013; Tilman & Downing, 1996; Yachi & Loreau, 1999). Although subject to some controversy (Allison, 2004; Caldeira et al., 2005; Downing & Leibold, 2010; Zhang & Zhang, 2006), this concept is known as the insurance hypothesis and postulates that ecosystem functioning and biodiversity are closely related, and that declines in biodiversity will result in ecosystem functioning being impaired by reducing ecosystem-level services and processes (Cardinale et al., 2009; Connolly et al., 2013; Fields et al., 1993; Hughes et al., 2003; Micheli & Halpern, 2005; Sanford, 1999; Yachi & Loreau, 1999). In diverse ecosystems, different species can perform analogous ecosystem functions under different environmental conditions, which

ensures that those functions persist even though some species are displaced (Ives & Carpenter, 2007; Tilman & Downing, 1996; Yachi & Loreau, 1999). Unfortunately, many coastal marine ecosystems present low functional redundancy (Micheli & Halpern, 2005), which implies that local loss of biodiversity will have substantial consequences at the community- and ecosystem-levels. In these ecosystems, species identity, functional traits and environmental setting often govern ecosystem functions and their response to disturbances (Emmerson et al., 2001; Goodsell & Underwood, 2008; Rossi et al., 2013; Rossi et al., 2009), and the loss of one or more key species, such as ecosystem engineers or keystone species, can overshadow the effect of species richness on ecosystem functions, resistance or resilience (Bolam et al., 2002; Coleman & Williams, 2002; Emmerson et al., 2001; Solan et al., 2004).

Ecosystem engineers

The term 'ecosystem engineer' was first coined by Jones et al. (1994, p. 374) in reference to 'organisms that directly or indirectly modulate the availability of resources (other than themselves) to other species, by causing physical state changes in biotic or abiotic material. In so doing they modify, maintain and/or create habitats'. There are essentially two types of engineers: those that alter the environment by 1) actively transforming non-living or living materials from one physical state to another or 2) passively changing habitats using their own physical structures. These organisms are called allogenic and autogenic engineers, respectively (Jones et al., 1994, 1997). Since the resources used by sympatric species are directly or indirectly controlled by physical state changes, engineering can have significant ecological consequences (Jones et al., 1997), and the loss of ecologically important engineers could have dramatic consequences on ecosystem functioning (Chapin III et al., 1997).

Climate change, and more particularly the effects of global warming, are capable of causing localised extinctions of ecosystem engineers, thereby inducing extensive indirect alterations to ecosystem structure and functioning (Chapin III et al., 1997; Peck et al., 2009). Although not dealing exclusively with ecosystem engineers, Koh et al. (2004) estimated that upon the loss of certain species, 6300 associated species would also become at risk of extinction, or become 'co-extinct'. A summary of studies reporting changes in environmental temperature altering ecosystem engineer biology is presented in Table 1. As evident in this table, warming-induced changes occurring at the organismal- and population-levels have been greatly studied with the majority of engineers displaying poleward range shifts and changes in physiology. However, most studies and models have disregarded the consequences of temperature mediated effects on engineers for community-level interactions, co-existing ecosystem engineers, and how alterations in *per capita* interaction strength of interacting ecosystem engineers alter their abundances over time, chains of extinction and ecosystem functioning.

Table 1: Summary of studies reporting effects of warming on ecosystem engineers.

Taxa	Main resources regulated	Location	Effects of warming	Reference
Marine plants: Macroalgae				
Ecklonia and *Sargassum* species	▪ Create habitat and shelter ▪ Protection from predators and desiccation ▪ Contribute to primary production [1]	Japan	Range contraction in temperate *Sargassum* and *Ecklonia* species and expansion in tropical *S. ilicifolium* due to warming	Tanaka et al. (2012)
Rocky shore macroalgae		Portugal	Northward expansion in range of warm-water species	Lima et al. (2007)
North Atlantic polar to cold-temperate macroalgae		Worldwide	Range extension into the High Arctic and retreat along the northeastern Atlantic coastline	Müller et al. (2009)
Temperate macroalgae		Australia	Range shift toward the poles in temperate species 25% decline in diversity predicted	Wernberg et al. (2011)
Marine plants: Seagrasses				
Posidonia oceanica and *Cymodocea nodosa*	▪ Contribute to primary production ▪ Modulate biogeochemical and sedimentary processes ▪ Act as breeding grounds and nurseries [2]	Balearic Islands, Spain	Reduced growth and leaf formation rates and leaf biomass per shoot: *P. oceanica*	Olsen et al. (2012)
Thalassia species		Gulf of Mexico and Caribbean	Beds denuded under highly elevated temperatures	Thorhaug et al. (1978)
Zostera marina		Virginia Coast Reserve	Bistability, or system with two stable equilibrium states, induced under higher temperatures and reductions in respiration and photosynthesis to a lesser extent	Carr et al. (2010)

[1] (Chung et al., 2011; Dijkstra et al., 2012; Gutierrez et al., 2011; Israel et al., 2010; Jueterbock et al., 2013; Watt & Scrosati, 2014; Wernberg et al., 2011; Wright et al., 2014)

[2] (Duarte & Chiscano, 1999; Hansen & Reidenbach, 2013; Hemminga & Duarte, 2000; Jones et al., 1994; Mouquet et al., 2013; Short & Wyllie-Echeverria, 1996; Smith, 1981)

Taxa	Main resources regulated	Location	Effects of warming	Reference
Terrestrial plants				
Betula pendula, *Fagus sylvatica*, *Galanthus nivalis*, *Forsythia suspensa*, *Quercus robur*, *Tilia platyphyllos* and *Sambucus nigra*	▪ Provide food and habitat ▪ Branches and leaves provide shade and reduce impacts of wind and rain ▪ Roots aerate soil and influence infiltration of water	Germany	Flowering advanced for *G. nivalis*, *F. suspensa* and *T. platyphyllos* Fruit ripening advanced for *S. nigra* Leaf colouring delayed in *Q. robur*, *F. sylvatica* and *B. pendula*	Menzel et al. (2001)
Trees at the International Phenological Gardens	▪ Dead leaves influence heat and gas exchange in soil habitat [3]	Europe	Between 1959-1996, leaf unfolding advanced by 6.3 days and leaf colouring delayed by 4.5 days	Menzel (2000)
Bivalves				
Cerastoderma edule and *Mya arenaria*	▪ Provide refuge from predation	Dutch Wadden Sea	Decline in recruitment following warm winters	Cardoso et al. (2009)
Mytilus californianus	▪ Stabilise sediment ▪ Deposit organic matter [4]	Oregon	Increased growth rate under higher temperature	Menge et al. (2008)
Reef- building corals				
Acropora cervicornis and *A. palmata*	▪ Provide habitat and shelter ▪ Produce and transform organic and inorganic materials [5]	Caribbean	Range extension toward the poles	Precht and Aronson (2004)
Oculina patagonica		Mediterranean Sea	Increased virulence of pathogen *Vibrio shiloi* at high temperature	Rosenberg and Ben - Haim (2002)
Pocillopora damicornis		Zanzibar, Africa	Extracellular proteinase (responsible for tissue lysis)	Ben - Haim and

[3] (Callaway & Walker, 1997; Facelli & Pickett, 1991; Holling, 1992; Jones et al., 1997; Juma, 1993)
[4] (Coleman & Williams, 2002; Crooks, 1998; Gutierrez et al., 2003; Karatayev et al., 2002; Reusch et al., 1994)
[5] (Bellwood & Hughes, 2001; Glynn, 2015; Gutierrez et al., 2011; Naumann et al., 2010; Rasheed et al., 2003; Wild et al., 2011; Wild et al., 2005)

Taxa	Main resources regulated	Location	Effects of warming	Reference
			expression at higher levels at high temperatures	Rosenberg (2002)
Zooxanthellae of reef-building coral species		Worldwide	Decline in abundance and increased extinction risk with increasing temperature	Carpenter et al. (2008)
Soil invertebrates				
Earthworm and termite species	▪ Form and maintain soil structure ▪ Influence the activity and diversity of organisms at lower trophic levels, structural heterogeneity and distribution of organic matter [6]	Worldwide	Changes in functional structure of earthworm communities, increase of endogeic populations and engineering occurring deeper in the soil	Lavelle et al. (1995)

[6] (Barois & Lavelle, 1986; Lavelle, Bignell, et al., 1997; Lavelle et al., 1995; Lavelle, Pashanasi, et al., 1997; Marinissen, 1995; Wood, 1996; Wood & Sands, 1978)

Temperature and engineer interactions

Temperature is strongly linked to distribution patterns due to its effects on organism physiology; species present a range of different thermal optima and limits (Hidalgo-Galiana et al., 2014; Hochachka & Somero, 2002; Somero, 2002), which will ultimately define thermal niches (Monahan & Tingley, 2012). For example, it is widely accepted that optimum growth occurs within a particular range of temperature, above and below which growth depreciates (Fong et al., 1997). Therefore, in ecological systems with multiple interacting species, temperature increases will determine thermal tolerance limits and thus the relative abundance of each species as well as the nature of biotic interactions (Somero, 2010). Indeed, many studies have demonstrated the importance of thermal stress in determining the latitudinal and vertical distribution of rocky intertidal animals, often involving one congener being replaced by another as a result of warming (Helmuth, 2009; Helmuth et al., 2006; Helmuth et al., 2002; Somero, 2002). Research on porcelain crabs, intertidal and subtidal snails as well as terrestrial ectotherms suggest that tropical species are more tolerant to heat than their temperate counterparts, although warming might pose a greater threat to congeners that are warm-adapted since their maximal habitat temperature could potentially reach or exceed the lethal temperature limit of the organism (Somero, 2010; Stenseng et al., 2005; Stillman, 2003; Tewksbury et al., 2008). Furthermore, those heat-tolerant congeners have a very limited capacity to increase their lethal temperature tolerance as a means of acclimatisation (Stillman, 2003). This will be no different for co-existing ecosystem engineers. However, as increased temperature favour tolerant species (Wood & McDonald, 1997), changes in dominant species are likely to result in phase shifts (Fig. 3).

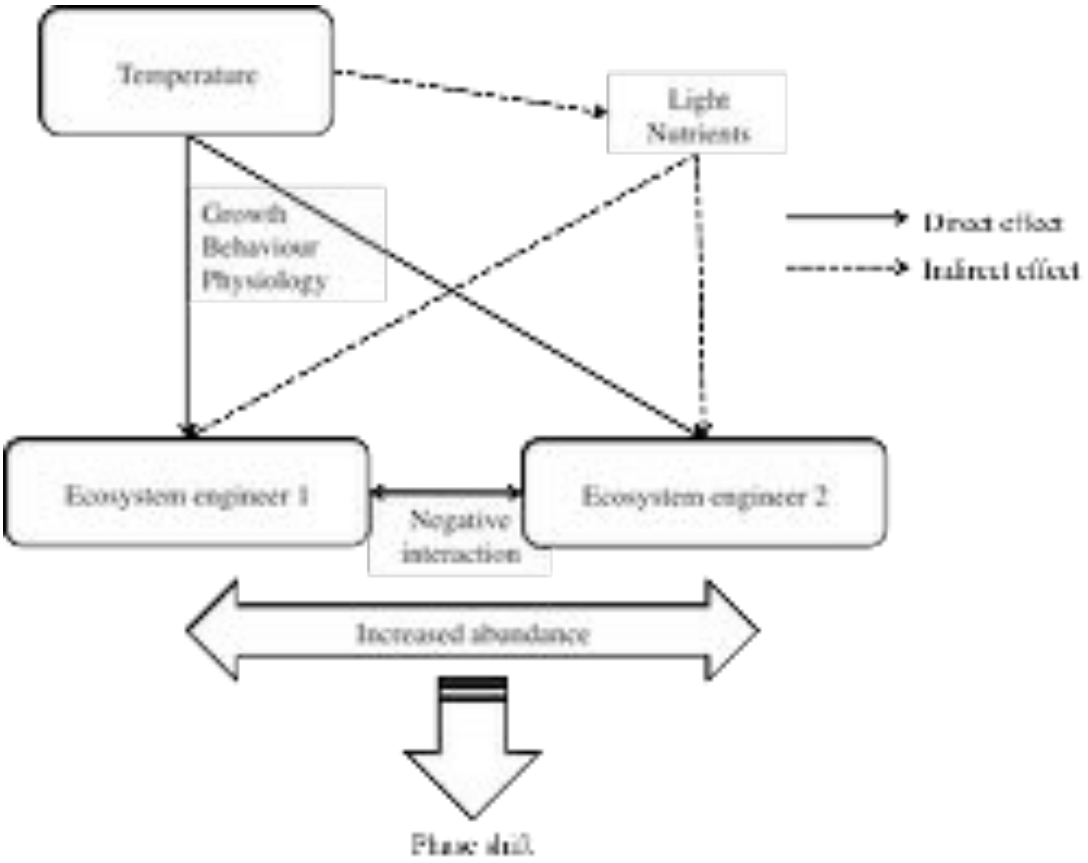

Figure 3: Conceptual model of the direct and indirect effects of temperature on two co-existing ecosystem engineers. Temperature directly and/or indirectly affects the abundance of the two species and their biological interactions, the outcome of which can ultimately lead to phase shift (one dominant engineer being replaced by another).

There is growing evidence demonstrating that ecosystems and the services they provide can be altered by human action and/or climate change, often resulting in less productive or otherwise less desired states (Folke et al., 2004; Scheffer & Carpenter, 2003). Such phase shifts, also known as regime shifts, are usually long lasting and challenging to reverse because of climate change and direct anthropogenic stressors, and are now being reported in a range of marine ecosystems, including coral reefs, kelp beds and seagrass meadows (Folke et al., 2004; Hughes, 1994; Ling et al., 2009; Montefalcone et al., 2015). In seagrass ecosystems, phase shifts cause a change in the dominance of different primary producers and typically involve the replacement of seagrasses by macroalgae (Montefalcone

et al., 2007; Montefalcone et al., 2015). Moreover, even if the primary stressor responsible for the phase shift is removed, seagrass might still not be able to recover due to secondary stressors such as increased turbidity and/or anoxic sediments (Unsworth et al., 2015). Another example of phase shift was documented in Jamaica where years of overfishing resulted in the progressive near-elimination of herbivorous fishes that regulated macroalgal growth; sea urchins *Diadema antilliarum* then became the primary herbivore thus performing similar functions, but populations were decimated following the *Diadema* die-off in the 1980s, which was responsible for the shift from coral- to macroalgal-dominated reefs. Ultimately, this loss of biodiversity reduced ecosystem resilience and prevented coral recovery (Hughes, 1994; Scheffer & Carpenter, 2003).

Seagrass meadows

Seagrasses are prominent constituents of the littoral zone in tropical and temperate regions, and greatly contribute to the primary production of the global ocean (Duarte & Chiscano, 1999; Smith, 1981). They modulate biogeochemical and sedimentary processes, as well as provide shelter and food for associated communities (Duarte & Chiscano, 1999). In addition, seagrass meadows are known to enhance biomass, biodiversity, primary and secondary production, and act as breeding grounds and nurseries for a number of finfish and shellfish populations (Duarte & Chiscano, 1999; Mouquet et al., 2013; Short & Wyllie-Echeverria, 1996). They also function as keystone habitats with high structural complexity (Duarte, 2002; Montefalcone et al., 2015; Short & Wyllie-Echeverria, 1996); they are thus described as foundation ecosystems in shallow coastal waters (Montefalcone et al., 2015). Unfortunately, seagrass-vegetated areas are declining worldwide (Short & Wyllie-Echeverria, 1996) with almost 30% of their known cover disappearing since 1879, placing them among

the most threatened ecosystems alongside coral reefs, mangroves and tropical rainforests (Waycott et al., 2009).

The widespread loss of seagrass meadows has largely been attributed to diverse natural and human-induced events (Short & Wyllie-Echeverria, 1996). Natural disturbances include any meteorological and geological events, such as prolonged or heavy rains, and coastal uplift and subsidence respectively, as well as shifts in biological interactions, such as grazing (Short & Wyllie-Echeverria, 1996). Human-induced disturbances, on the other hand, typically include events that result in a decrease in water clarity, the release of toxic compounds into coastal waters, any direct mechanical damage, but also indirect impacts caused by global anthropogenic changes (i.e. global warming, rise in sea level etc.) (Duarte, 2002; Short & Wyllie-Echeverria, 1996; Walker et al., 1989). Overall, these types of disturbances are thought to have impacted more than 65% of seagrass and wetland habitats and have exhausted more than 90% of essential species (Lotze et al., 2006).

Research Aims and Questions

In Africa, seagrasses generally suffer from a lack of research, particularly on the west coast (Waycott et al., 2009). Locally, significant losses of seagrass, estimated at 38%, were reported in Langebaan Lagoon over the last 50 years (Pillay et al., 2010). Seagrass declines have been associated with increased sediment loads caused by dredging operations in Saldanha Bay (Angel et al., 2006) as well as bait collecting and trampling, particularly in areas open to recreation and bait harvesting. Yet, seagrass declines have been recorded in areas restricted from human activity, albeit at lower rates (Pillay et al., 2010), suggesting that processes beyond human disturbances likely contribute to observed declines.

Air temperature data collected by the South African Weather Service (SAWS) near Langebaan Lagoon and in Geelbek, which is located at the southern end of the system,

indicate that temperature has been rising over the past few decades (Fig. 4), which could have in turn affected water temperature to a certain degree. As a result, one could theorise that seagrass losses are linked directly or indirectly to increasing temperatures. In parallel with the large decline in *Zostera capensis* cover observed in recent years, the red coarsely branched macroalga *Gracilaria gracilis* has become seemingly more abundant in areas that were previously dominated by *Z. capensis*. In Langebaan Lagoon, *G. gracilis* can accumulate in large mats within the seagrass beds or as drift on the low shore. This increased macroalgal presence has an unknown impact on *Z. capensis* although studies have demonstrated the deleterious effects of other drift species on seagrass beds (Höffle et al., 2011; Huntington & Boyer, 2008), implying that *G. gracilis* could somehow contribute to the demise of *Z. capensis*. Lastly, based on observations of *G. gracilis* colonising beds of *Z. capensis* and knowledge that macroalgae are positively affected by light and temperature (Fong & Harwell, 1994), one could also theorise a link between rising temperatures and increases in macroalgae individually or interactively contributing to declines in *Z. capensis* cover.

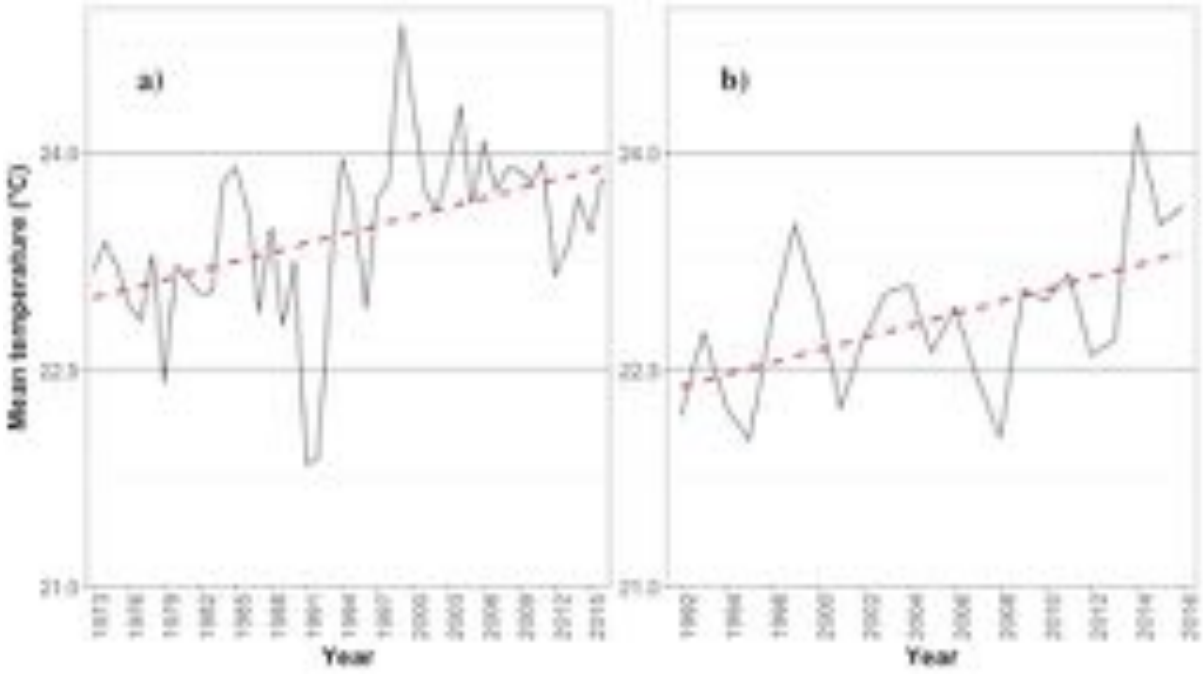

Figure 4: Yearly maximum temperature recorded at stations a) near Langebaan Lagoon and b) Geelbek. Note temperature data were missing in Geelbek between 1995-1996. The red dashed lines

represent the linear regression and show that air temperature has increased over the last few decades in both datasets.

Considering the role of seagrass meadows as keystone habitats and the limited research on the causes of *Z. capensis* losses, this study aims to quantify the individual and interactive effects of *G. gracilis* and increasing temperatures on the performance of *Z. capensis*. This study therefore contributes to predicting the future distributions of these two ecosystem engineers in Langebaan Lagoon and grows existing knowledge on *Z. capensis*.

Materials and Methods

Site description

Samples of macroalgae and seagrasses were collected from Klein Oesterwal ($33°7'14"S$ and $18°3'09"E$) at Langebaan Lagoon, which is located on the Atlantic coast of South Africa, about 96 km north of Cape Town, between $33°11'27"S$, $18°07'37"E$ and $17°58'07"E$ (Christie & Moldan, 1977; Day, 1959; Pillay et al., 2010) (Fig. 5).

Figure 5: Location of Langebaan Lagoon and Klein Oesterwal (using QGIS). Inset shows location of the Saldanha Bay-Langebaan Lagoon complex within South Africa. Dashed lines represent approximate positions of human-management zone boundaries.

Langebaan Lagoon forms part of Saldanha Bay, which is the only large natural harbour on the west coast of South Africa. The system experiences limited wave action, which is thought to enhance local diversity (Christie & Moldan, 1977; Shannon & Stander, 1977). The lagoon was proclaimed a national park in 1985, but is also recognised by the Ramsar Convention as a wetland of international importance, and by BirdLife International as an Important Bird Area (Pillay et al., 2010). The lagoon is approximately 15 km long, 4 km wide (at widest point) and the depth does not exceed 10 m (1.8 m at low tide) (Christie & Moldan, 1977; Day, 1959). The system comprises tidal channels, subtidal flats, submerged sandbanks, intertidal flats, and salt marshes (Flemming, 1977). In addition, it is divided into three zones: a multi-purpose recreational area on the north, a limited recreational area, and a

sanctuary area with prohibited access in the southern end of the lagoon (Pillay et al., 2010; South African National Parks, 2013) (Fig. 5).

The lagoon is one of the few areas in the Benguela region that supports a large number of primary producers, with dense beds of *Gracilaria gracilis* (Stackhouse) Steentoft, Irvine et Farnham and *Zostera capensis* Setchell (Gibson et al., 2007). The main primary producers of the area consist of the macroalga and the seagrass, which are found in high abundance (Gibson et al., 2007). Drift algae and epiphytes are intrinsic components of seagrass beds and largely contribute to their ecology (da Silva & Asmus, 2001). Albeit beyond the scope of this study, other primary producers in the lagoon include *Sarcocornia* and *Spartina* species, which are found in the southern half of the lagoon (Gibson et al., 2007).

Species description

Both *Zostera capensis* and *Gracilaria gracilis* are found on sandflats below mid-tide, which can either be bare or covered to different degrees by these two species (Day, 1959; Molloy & Bolton, 1995).

Gracilaria gracilis, also known as *G. verrucosa* in South Africa (Bird et al., 1994; Critchley, 1993; Iyer et al., 2004; Steentoft et al., 1995), is a corticated red alga (Family: Rhodophyta), which is found across the globe, except in the Arctic Ocean (Raikar et al., 2001; Sidik et al., 2001). In southern Africa, the species can be found from Port Elizabeth, South Africa, to Lüderitz, Namibia (Iyer et al., 2004; Iyer et al., 2005; John et al., 2004; Price et al., 1988) (Supp. Fig. 1-2), where it grows at low tide level in shallow sandy bays (Siegfried, 1994) and where the average annual temperature approximates 15°C. In Saldanha Bay-Langebaan Lagoon, populations of *Gracilaria* are described as commercially viable and the macroalga covers a substantial area of the lagoon, mainly near the mouth (Rothman et al.,

2009), even though temperatures are described as sub-optimal (Simons, 1977; Wilson & Critchley, 1997). 25℃ is considered the optimum growth temperature for *G. gracilis* (Engledow & Bolton, 1992; McLachlan & Bird, 1984; Molloy & Bolton, 1995).

While *G. gracilis* has been extensively studied due to its high commercial value, in the fabrication of agar (de Zaixso, 1987; Raikar et al., 2001), there is a substantial gap in knowledge on the Cape eelgrass *Zostera capensis*. The Cape eelgrass is a marine flowering plant (Short et al., 2007) commonly found in sheltered bays and estuaries on the coast of southern Africa, in both the intertidal and shallow subtidal zones, where its upper limit could be controlled by dessiccation (Angel et al., 2006; Whitfield et al., 1989; Wortmann et al., 1997), and occurs from Saldanha Bay, South Africa, to Kenya (Hanekom & Baird, 1988; Short et al., 2010) (Supp. Fig. 1-2). It is listed as vulnerable under the IUCN Red List of Threatened Species as a result of habitat fragmentation and a decrease in habitat quality (Short et al., 2010). *Zostera capensis* occurs on various intertidal banks, mainly on muddy sediment, and is described as being very patchy, although it can flourish at the southern end of the lagoon (Day, 1959).

Pre-experimental procedure

A total of 54 plant pots (area ≈ 132.7 cm^2, depth = 10.8 cm, bottom diameter = 10.8 cm, top diameter = 13 cm) were filled with cores of sand and seagrasses from extensive shallow water seagrass meadows at low tide. All cores were collected using stainless steel corers (depth = 32.8 cm, diameter = 10.2 cm). Clumps of *Gracilaria* were collected by hand in the area from which seagrass cores were collected. Random sampling was employed when collecting macroalgae and seagrasses to ensure spatial independence (Burdick & Kendrick, 2001). Samples were transported to the laboratory in large boxes then placed randomly in

tanks filled with seawater (35‰). All samples were acclimatised by gradually increasing the water temperature over the course of four days, until the desired temperature was reached (18°C, 22°C and 30°C). Prior to the commencement of the experiment, any mesograzers and visible indications of rot or seagrass blades on *Gracilaria* were removed.

Experimental design

To determine the effects of temperature and levels of *Gracilaria* on the performance of *Z. capensis,* three different temperature treatments were used (18°C, 22°C and 30°C) and three levels of macroalga (no *Gracilaria,* 1.2 g and 2.3 g) were used per temperature treatment based on ranges recorded naturally in the study site, over a period of seven weeks. High and low macroalgal biomass treatments contained 2.3 g and 1.2 g of *G. gracilis*, respectively. The experiment design was adapted from Höffle et al. (2011) and Waspe (2015) (Fig. 6). All replicates used in the experiment were randomly interspersed. Three header tanks (120L) were filled with seawater and individually heated to the designated temperatures (18°C, 22°C and 30°C) using aquarium heaters (300W Eheim Jager). The temperature levels used in the experiment were based on water temperature data collected from five sites in Langebaan Lagoon, over a year, with an observed minimum temperature of 12.74°C and a maximum of 28.28°C. Temperature levels in the mid- to upper range of recorded water temperatures were tested in the experiment given the warming trend observed in the lagoon and the need to understand the latter effects on seagrasses. Water from header tanks was then pumped (submersible pump Atman PH-2500) into three interconnected tanks (80L) and back into the header tank. All samples were provided with artificial daylight (Osram Biolox L58W/965 and Philips Master TL-D De Luxe 58W/965) at a 12:12 day/night period mounted about one meter above the tanks.

Two pots per level of *Gracilaria* were placed within individual 80L tanks; resulting in a total of six plant pots being positioned in every tank (Fig. 6). There were three replicate tanks per temperature treatment. Seagrass shoot density was not standardised between or within treatments due to the sensitivity of *Z. capensis* to transplantation and experimental manipulation (Chenoweth et al., 2016). To overcome potential problems with variation in seagrass density, all pots were randomly allocated to treatments.

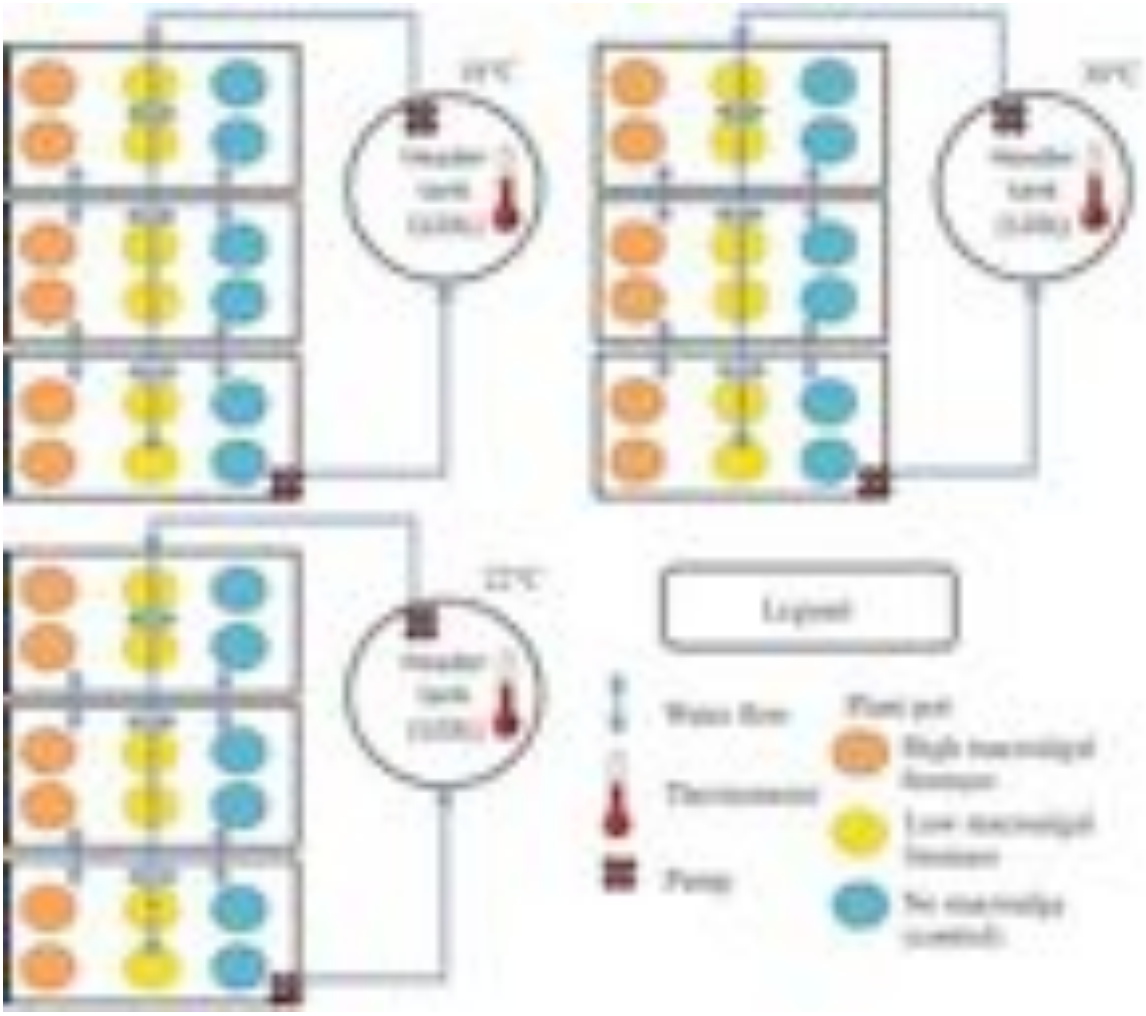

Figure 6: Experimental design testing the interactive effects of temperature and additions of *Gracilaria* on the performance of *Z. capensis*. Note that pots were randomly interspersed and not spatially aligned.

Water temperature was recorded daily to ensure that desired levels were maintained per temperature treatment. Oxygen levels (YSI DO200, Portable Dissolved Oxygen and Temperature Instrument), pH (Sera pH-Test) and nutrient levels (Sera Nitrite-Test (NO_2), Sera Nitrate-Test (NO_3), and Sera Ammonium/Ammonia-Test (NH_4/NH_3)) were randomly measured in an individual tank per temperature treatment; every three days for dissolved oxygen, and once a week for pH and nutrient levels. All tanks were cleaned roughly once a week in order to remove epiphytes growing on tank walls and dead seagrass leaves.

Data collection

Seagrass shoot density

Seagrass shoot density was quantified at the beginning and end of the experiment by counting all shoots present in each plant pot.

Seagrass leaf length, width and area

At the termination of the experiment, three to five leaves were harvested randomly across the spread of seagrass patches, from which widths were recorded at the base, middle and top of each leaf using a vernier calliper. Averaged values were used to calculate the surface area of the leaves (Short & Duarte, 2001; Waspe, 2015).

Fouling of seagrass leaves by microalgae

The degree of fouling of seagrass leaves was measured at the end of the experiment using the leaves from which length, width and surface area were estimated. Leaves were washed under flowing water to remove any loosely attached epiphytes, inorganic particles as well as salt (Kendrick & Lavery, 2001). This was followed by large epiphytes being removed by forceps and remaining epiphytes by a microscope slide. All epiphytes were placed in pre-weighed aluminium cups, which were weighed first (nearest 0.0001 g), dried at 60°C for 48 hours, and weighed again. Epiphyte biomass was expressed as the difference in biomass before and after drying, and was expressed as g (dry weight).

Senescent versus non-senescent, and below-ground biomass

All seagrass material was collected at the end of the experiment from each plant pot, rinsed with freshwater to remove dead tissue, sediment, and debris, and then separated into above-ground (leaves and sheaths) and below-ground (rhizomes and roots) material. All above-ground material was categorised as either senescent (brown colour) or non-senescent (green colour). The dried weight of senescent, non-senescent and below-ground material was then recorded. All samples were placed in pre-weighed aluminium dishes, dried at 60°C for 48 hours and then weighed again (Duarte & Kirkman, 2001; Garthwin et al., 2014; Olsen et al., 2012). Biomass was expressed as g (dry weight) and was recorded to the nearest 0.0001 g.

Gracilaria biomass and percent cover

To measure biomass of *Gracilaria* at the end of the experiment, samples were rinsed and blotted with paper towels to remove excess water and then weighed (Raikar et al., 2001; Rothman et al., 2009). The biomass was expressed as a g (wet weight) and was recorded to the nearest 0.0001 g. All fragments of *Gracilaria* per plant pot were then placed in a large glass beaker of a size similar to experimental pots. The approximate area of the glass beaker occupied by *Gracilaria* was used as an indicator of percent cover of this macroalga in each pot.

Gracilaria fouling

All fragments of *G. gracilis* from each experimental pot were transferred to 50 mL vials and stored in 70% ethanol-rose Bengal solution for at least 24 hours. *G. gracilis* fragments were then viewed under a stereo microscope (Leica EZ4 D) and the degree of

fouling scored qualitatively at five different locations. Fouling scores ranged from 1 to 5, with 1 indicating no epiphyte fouling and 5 denoting heavy fouling (Fig. 7). The five scores were averaged to calculate the overall fouling of *G. gracilis* per pot.

Figure 7: Fouling levels of *Gracilaria gracilis* and associating qualitative scores: a-b were scored 1 (not fouled); c-d obtained a score of 2; e-f = 3; g-h = 4; and i-j = 5 (heavily fouled).

Statistical analyses

The individual and interactive effects of temperature and additions of *Gracilaria gracilis* were tested with two-way ANOVAs using the software environment R (R Core Team, 2013). Homogeneity of variance and normality were tested using Levene's test and Shapiro-Wilk test, respectively, along with boxplots, histograms and residual plots, which are considered more informative in checking assumptions (Quinn & Keough, 2002). If required, data were cube root transformed. The latter transformation was applied to seagrass fouling, and senescent and below-ground biomass. For balanced designs, hypotheses were estimated and tested using Type I Sum of Squares (SS), while Type III SS were used for unbalanced designs caused by random loss of observations. Post-hoc pairwise comparisons among treatment means were performed if significant differences were detected between the means using Tukey tests.

A permutational multivariate ANOVA (PERMANOVA) was also conducted (using PRIMER v6) to explore differences in seagrass characteristics (e.g. growth, fouling, leaf width, length and area) across temperature and macroalgal treatments, and to determine any interactions between those two factors. Untransformed, normalised variables were used to generate resemblance matrices. Homogeneity of multivariate dispersion was determined using the permutational analysis of multivariate dispersions (PERMDISP). All analyses were based on a Euclidean similarity index and because of the unbalanced data, a Type III PERMANOVA was conducted as it is considered to produce a more conservative analysis (Anderson et al., 2008). The level of significance was set at $\alpha = 0.05$ for all tests.

Results[7]

The non-metric multidimensional scaling (MDS) ordination (Fig. 8) in combination with PERMANOVA indicated significant differences in seagrass performance among different temperatures ($Pseudo\ F_{2,17} = 3.3885; p = 0.001$; Table 2), but not between *Gracilaria* treatments ($Pseudo\ F_{2,17} = 0.7444; p = 0.677$) or the interaction between temperature and *Gracilaria* ($Pseudo\ F_{4,17} = 0.2934; p = 1$). Figure 8 displays a homogeneous cluster for seagrasses at 18℃ and 22℃, indicating similarities between them, while those subjected to 30℃ were distinct from the latter group. However, no differentiation can be observed among macroalgal treatments. Pairwise tests (Table 3) confirmed that seagrasses at 30℃ contrasted significantly from those at 18℃ and 22℃ (for 18-30: $t = 2.133; p = 0.002$, and for 22-30: $t = 2.2142; p = 0.004$) and that seagrass performance subjected to the latter temperatures were statistically similar ($t = 0.4544; p = 0.927$). Vector overlays indicated that greater shoot density, fouling, leaf width, length and area together with senescent and non-senescent biomass were the main seagrass response variables distinguishing seagrasses exposed to 30℃ from other temperature treatments. Although the trend was not strong, seagrasses from the lower temperature treatments were characterised by having slightly greater below-ground biomass (Fig. 8). The stress value of 0.14 indicates a fairly good fitting solution.

[7] Refer to Supplementary Table 1 for mean ($\pm$ SE) values

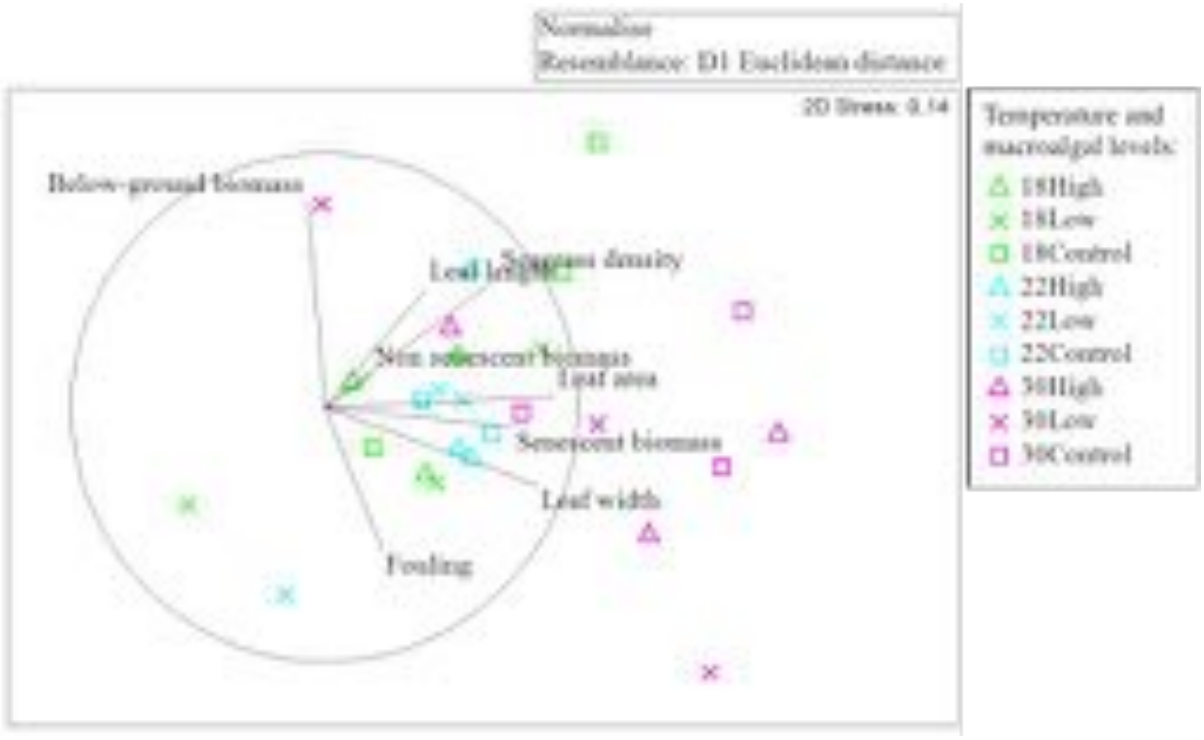

Figure 8: Non-metric MDS ordination plot presenting dissimilarities between seagrass samples under different temperature and *Gracilaria* treatments. Vector overlays identify seagrass response variables that discriminated between treatments. In the legend, 18, 22 and 30 refer to temperature treatments; High = high macroalgal biomass, Low = low macroalgal biomass, and Control = no *Gracilaria* added.

Table 2: Results of Multifactor PERMANOVA assessing the individual and interactive effects of temperature and macroalgal levels on seagrass performance. Significant results ($p < 0.05$) are highlighted in **bold**. PERMDISP: $F_{2,23} = 2.065$; $p = 0.245$.

Source of variation	Df	SS	Pseudo-F	p
Temperature	2	50.994	3.389	**0.001**
Gracilaria levels	2	11.203	0.744	0.677
Temperature × *Gracilaria*	4	8.835	0.294	1
Residuals	17	127.92		

Table 3: Results of Multifactor PERMANOVA pairwise tests exploring differences in seagrass characteristics between temperature treatments. Significant results ($p < 0.05$) are highlighted in **bold**.

Temperature groups	t-statistic	p
18 – 22	0.454	0.927
18 – 30	2.133	**0.002**
22 – 30	2.214	**0.004**

Seagrass shoot density

Temperature ($F_{2,18} = 1.568; p = 0.236$), macroalgal levels ($F_{2,18} = 0.323; p = 0.728$) and their interaction ($F_{4,18} = 0.473; p = 0.755$) did not significantly affect seagrass shoot density (Table 4; Fig. 9).

Table 4: Two-way ANOVA results assessing the individual and interactive effects of temperature and macroalgal levels on seagrass shoot density. Significant results ($p < 0.05$) are highlighted in **bold**. Levene's test $F_{8,18} = 0.284; p = 0.963$.

Source of variation	Df	SS	F	p
Temperature	2	80.3	1.568	0.236
Gracilaria levels	2	16.5	0.323	0.728
Temperature × *Gracilaria*	4	48.5	0.473	0.755
Residuals	18	460.8		

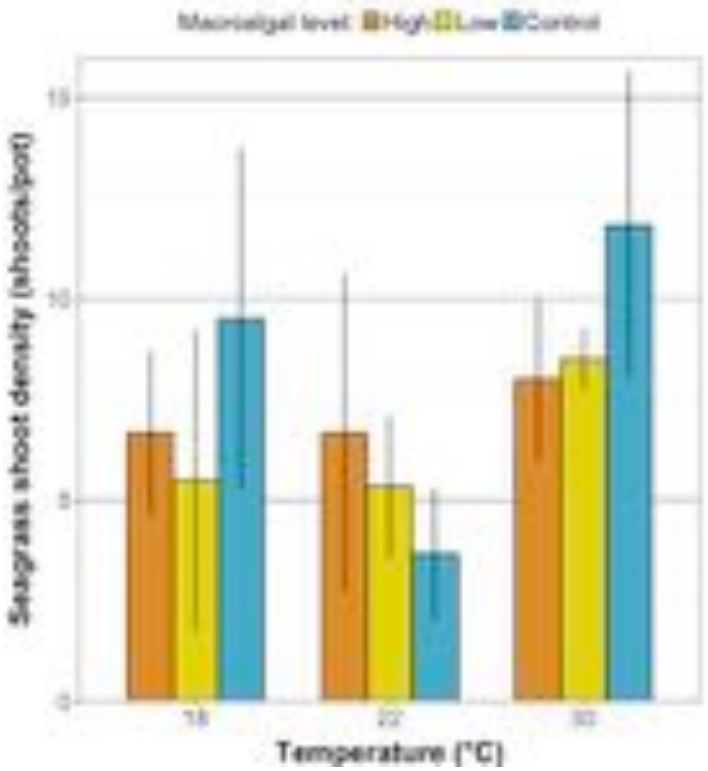

Figure 9: Seagrass shoot density across three different temperature treatments and three *Gracilaria* levels. Columns represent mean values ± 1 SE, n = 3.

Seagrass leaf length, width and area

There were no individual or interactive significant effects of temperature and *Gracilaria* treatments on leaf length (Table 5a). Despite the lack of statistically significant effects, trends suggest a negative effect of temperature and *Gracilaria* on leaf length, particularly at 18℃ (Figure 10a).

There were significant effects of temperature on leaf width ($F_{2,17} = 14.271; p = 0.0002$; Table 5b), with width at 30℃ being significantly greater than at 18℃ and 22℃ ($p_{18-30} < 0.001$ and $p_{22-30} = 0.002$). However, leaf width was not different between 18℃ and 22 ℃ ($p = 0.833$; Table 6a). *Gracilaria* treatments and the interaction between temperature and *Gracilaria* did not significantly affect leaf width ($p > 0.5$; Fig. 10b).

No significant effects of *Gracilaria* treatments and the interaction between temperature and *Gracilaria* treatments were observed for seagrass leaf area. Temperature, on the other hand, had a marginally non-significant effect ($F_{2,17} = 3.167; p = 0.068$) on area (Table 5c). Post-hoc Tukey tests showed the greatest, but not significant, mean leaf area difference between 18℃ and 30℃ ($p = 0.086$; Table 6b).

Table 5: Two-way ANOVA results assessing the individual and interactive effects of temperature and macroalgal levels on seagrass leaf length, width and area. Significant results ($p < 0.05$) are highlighted in **bold**.

Source of variation	Df	SS	F	p
a) Leaf length				
Levene's test: $\boldsymbol{F_{8,17} = 0.416; p = 0.896}$				
Temperature	2	4.66	0.567	0.578
Gracilaria levels	2	12.20	1.485	0.255
Temperature × *Gracilaria*	4	4.40	0.268	0.895
Residuals	17	69.87		
b) Leaf width				
Levene's test: $\boldsymbol{F_{8,17} = 0.657; p = 0.721}$				
Temperature	2	0.020	14.271	**0.0002**
Gracilaria levels	2	0.0002	0.159	0.855
Temperature × *Gracilaria*	4	0.0008	0.295	0.877
Residuals	17	0.012		
c) Leaf area				
Levene's test: $\boldsymbol{F_{8,17} = 0.257; p = 0.972}$				
Temperature	2	0.838	3.167	0.068
Gracilaria levels	2	0.298	1.125	0.348
Temperature × *Gracilaria*	4	0.189	0.357	0.836
Residuals	17	2.251		

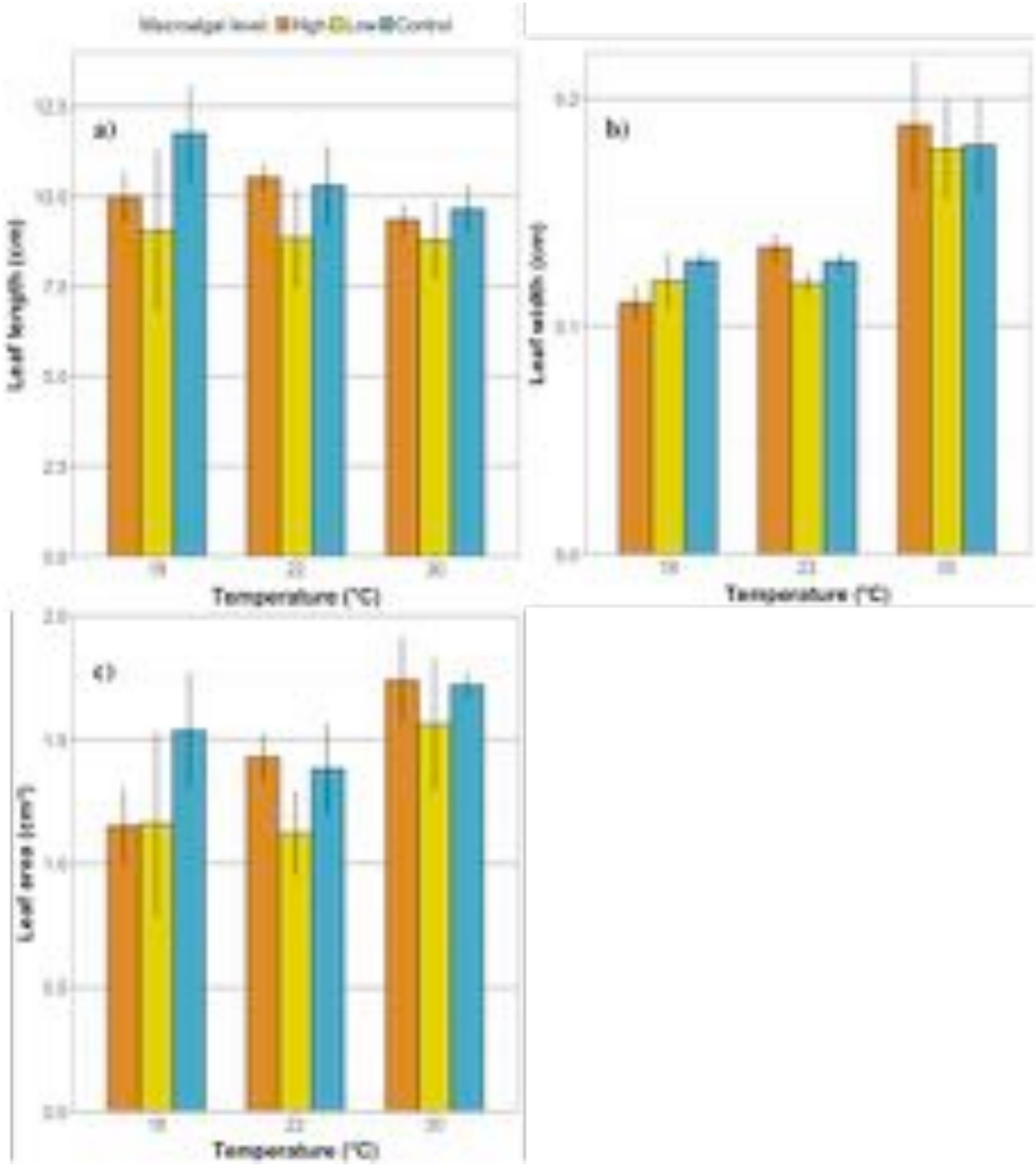

Figure 10: Seagrass leaf a) length, b) width, and c) area across three temperatures and three *Gracilaria* levels. Columns represent mean values ± 1 SE, n = 3.

Table 6: Tukey's pairwise comparison of group means in a) leaf width and b) leaf area between temperature treatments. Significant results ($p < 0.05$) are highlighted in **bold**.

Temperature groups	Mean difference	p
	a) Leaf width	
18 – 22	-0.01	0.717
18 – 30	-0.06	**< 0.001**
22 – 30	-0.06	**0.002**
	b) Leaf area	
18 – 22	-0.0200	0.993
18 – 30	-0.3911	0.086
22 – 30	-0.3711	0.120

Fouling of seagrass leaves by microalgae

Temperature had a significant effect on the fouling (cube root transformed) of seagrass leaves ($F_{2,17} = 10.320; p = 0.001$; Table 7). While the difference in mean fouling was not significantly different between 18℃ and 22℃ ($p = 0.980$), the leaves in the 30℃ were significantly more fouled than at 18℃ and 22℃ ($p_{18-30} = 0.004$ and $p_{22-30} = 0.03$; Table 8). In addition, although *Gracilaria* did not have any single or interactive significant effect, visual patterns suggest that low levels of *Gracilaria* were associated with more fouling than high or control levels of macroalga (Fig. 11).

Table 7: Two-way ANOVA results assessing the individual and interactive effects of temperature and macroalgal levels on the fouling of seagrass leaves (cube root transformed). Significant results ($p < 0.05$) are highlighted in **bold**. Levene's test: $F_{8,17} = 0.730; p = 0.664$.

Source of variation	Df	SS	F	p
Temperature	2	0.020	10.320	**0.001**
Gracilaria levels	2	0.004	1.916	0.178
Temperature × *Gracilaria*	4	0.0003	0.077	0.989
Residuals	17	0.017		

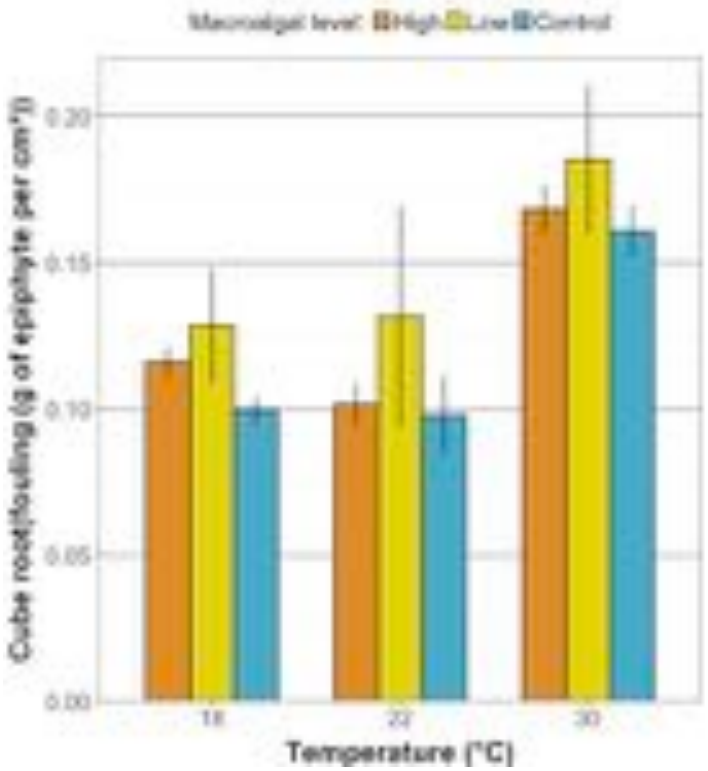

Figure 11: Seagrass fouling (cube root transformed) across three temperature treatments and three *Gracilaria* levels. Columns represent mean values ± 1 SE, n = 3.

Table 8: Tukey's pairwise comparison of group means in fouling (cube root transformed) of seagrass leaves between temperature treatments. Significant results ($p < 0.05$) are highlighted in **bold**.

Temperature groups	Mean difference	p
18 – 22	0.0029	0.980
18 – 30	-0.0566	**0.004**
22 – 30	-0.0595	**0.003**

Senescent versus non-senescent, and below-ground biomass

There was a significant effect of temperature on seagrass senescent biomass ($F_{2,18} = 22.921; p < 0.001$), with an increase in senescent biomass associated with rising temperature. Mean senescent biomass was statistically greater at 30℃ ($p_{18-30} < 0.001$ and $p_{22-30} < 0.001$) while being similar between 18℃ and 22℃ ($p_{18-22} = 0.566$; Table 9a and 10; Fig. 12a). In contrast, *Gracilaria* levels and its interaction with temperature did not

significantly affect senescent biomass (levels of *Gracilaria*: $F_{2,18} = 0.390; p = 0.683$ and the interaction: $F_{4,18} = 0.297; p = 0.876$).

Temperature and *Gracilaria* additions did not have any significant individual or interactive effects on non-senescent biomass ($p > 0.5$; Table 9b; Fig. 12b). Similarly, seagrass below-ground biomass was affected by neither temperature, *Gracilaria* levels nor their interaction ($p > 0.5$; Table 9c; Fig. 12c).

Table 9: Two-way ANOVA results assessing the individual and interactive effects of temperature and macroalgal levels on seagrass senescent (cube root transformed) and non-senescent, as well as below-ground (cube root transformed) biomass. Significant results ($p < 0.05$) are highlighted in **bold**.

Source of variation	Df	SS	F	p
a) Senescent biomass (cube root transformed)				
Levene's test: $\boldsymbol{F_{8,18} = 0.370; p = 0.923}$				
Temperature	2	0.048	22.921	$\mathbf{1.126 \times 10^{-5}}$
Gracilaria levels	2	0.0008	0.390	0.683
Temperature × *Gracilaria*	4	0.001	0.297	0.876
Residuals	18	0.019		
b) Non-senescent biomass				
Levene's test: $\boldsymbol{F_{8,18} = 0.619; p = 0.751}$				
Temperature	2	3.00×10^{-8}	0.071	0.932
Gracilaria levels	2	1.25×10^{-7}	0.295	0.748
Temperature × *Gracilaria*	4	2.49×10^{-7}	0.294	0.878
Residuals	18	3.81×10^{-6}		
c) Below-ground biomass (cube root transformed)				
Levene's test: $\boldsymbol{F_{8,18} = 0.644; p = 0.732}$				
Temperature	2	0.0014	1.320	0.292
Gracilaria levels	2	0.0005	0.474	0.630
Temperature × *Gracilaria*	4	0.0007	0.352	0.839
Residuals	18	0.0093		

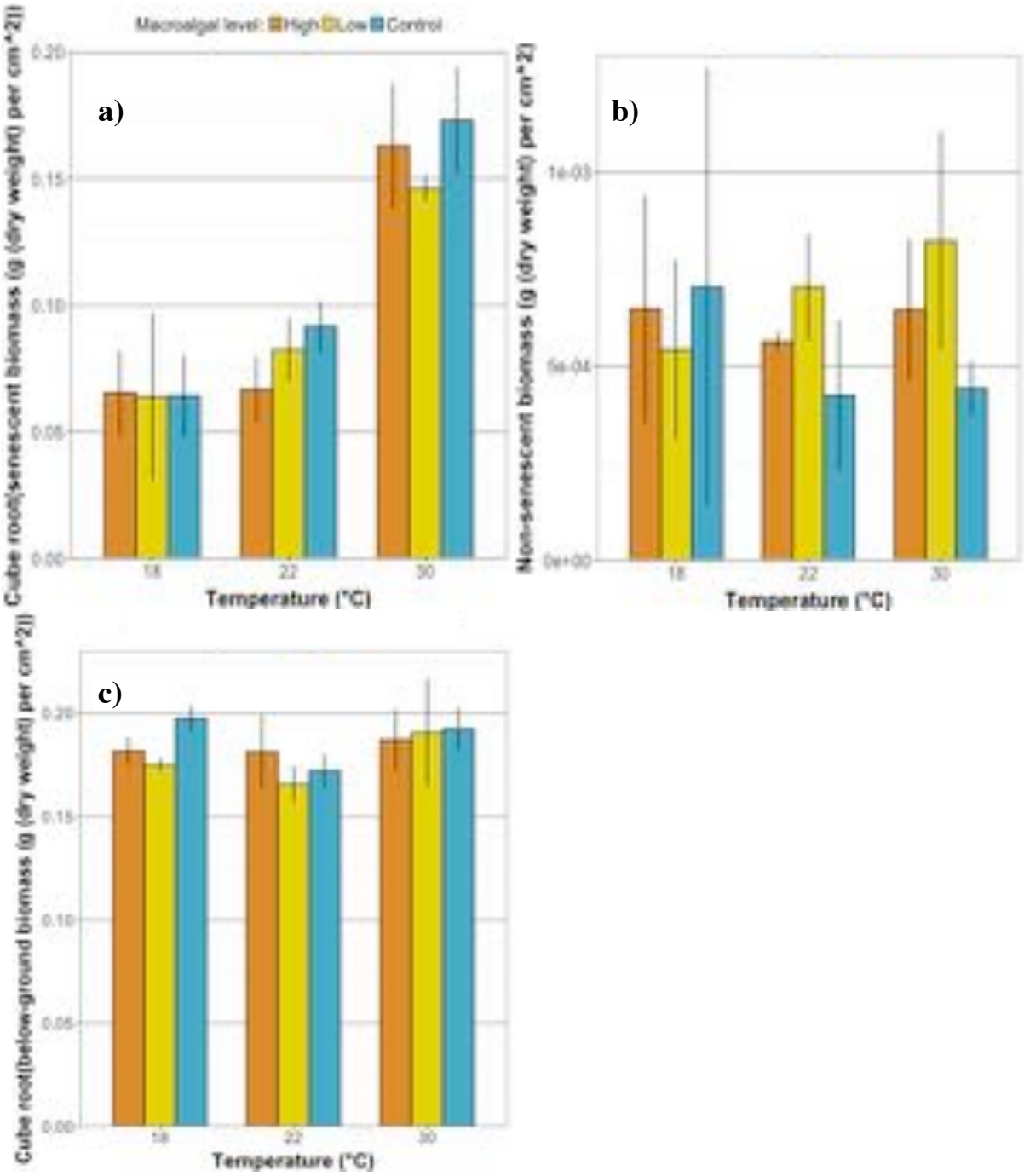

Figure 12: Seagrass a) senescent (cube root transformed), b) non-senescent, and c) below-ground (cube root transformed) biomass across three temperature treatments and three *Gracilaria* levels. Columns represent mean values ± 1 SE, n = 3.

Table 10: Tukey's pairwise comparison of group means in senescent biomass (cube root transformed) between temperature treatments. Significant results ($p < 0.05$) are highlighted in **bold**.

Temperature groups	Mean difference	p
18 – 22	-0.0158	0.566
18 – 30	-0.0962	**< 0.001**
22 – 30	-0.0805	**< 0.001**

Gracilaria biomass and percent cover

The final biomass of *G. gracilis* was significantly affected by temperature ($F_{2,12} = 56.668; p = 7.700\times10^{-7}$) and *Gracilaria* treatments ($F_{1,12} = 49.014; p = 1.430 \times 10^{-5}$; Table 11a). Macroalgal biomass at 18 ℃ was significantly lower than at 22 ℃ ($p_{18-22} < 0.001$) and 30℃ ($p_{18-30} < 0.001$) relative to 18℃, but did not differ significantly between 22℃ and 30℃ ($p_{22-30} = 0.348$; Table 12a). Across all temperature treatments, macroalgal biomass was greater in the high than low *Gracilaria* level ($p < 0.001$; Fig. 13a).

The percent cover of *Gracilaria* was affected by the main effects of temperature ($F_{2,12} = 9.013; p = 0.004$) and *Gracilaria* treatments ($F_{1,12} = 5.978; p = 0.031$) as well as their interaction ($F_{2,12} = 4.734; p = 0.031$; Table 11b). The lowest percent cover was found at 18℃ and differed marginally from 22℃ ($p_{18-22} = 0.057$) but significantly from 30℃ ($p_{18-30} = 0.003$; Table 12b). However, coverage was relatively similar between 22℃ and 30℃ ($p = 0.276$; Table 12b). In addition, macroalgal cover was predictably greater at high than low levels of macroalga ($p_{L-H} = 0.031$).

Table 11: Two-way ANOVA results assessing the individual and interactive effects of temperature and macroalgal levels on *Gracilaria* biomass and percent cover at the end of the experiment (t = 7 weeks). Significant results ($p < 0.05$) are highlighted in **bold**.

Source of variation	Df	SS	F	P
a) *Gracilaria* biomass Levene's test: $\boldsymbol{F_{5,12} = 0.341; p = 0.878}$				
Temperature	2	0.00033	56.668	$\mathbf{7.700 \times 10^{-7}}$
Gracilaria levels	1	0.00014	49.014	$\mathbf{1.430 \times 10^{-5}}$
Temperature × *Gracilaria*	2	0.000004	0.683	0.524
Residuals	12	0.00004		
b) *Gracilaria* percent cover Levene's test: $\boldsymbol{F_{5,12} = 0.231; p = 0.942}$				
Temperature	2	1433.3	9.013	**0.004**
Gracilaria levels	1	475.3	5.978	**0.031**
Temperature × *Gracilaria*	2	752.8	4.734	**0.031**
Residuals	12	954.2		

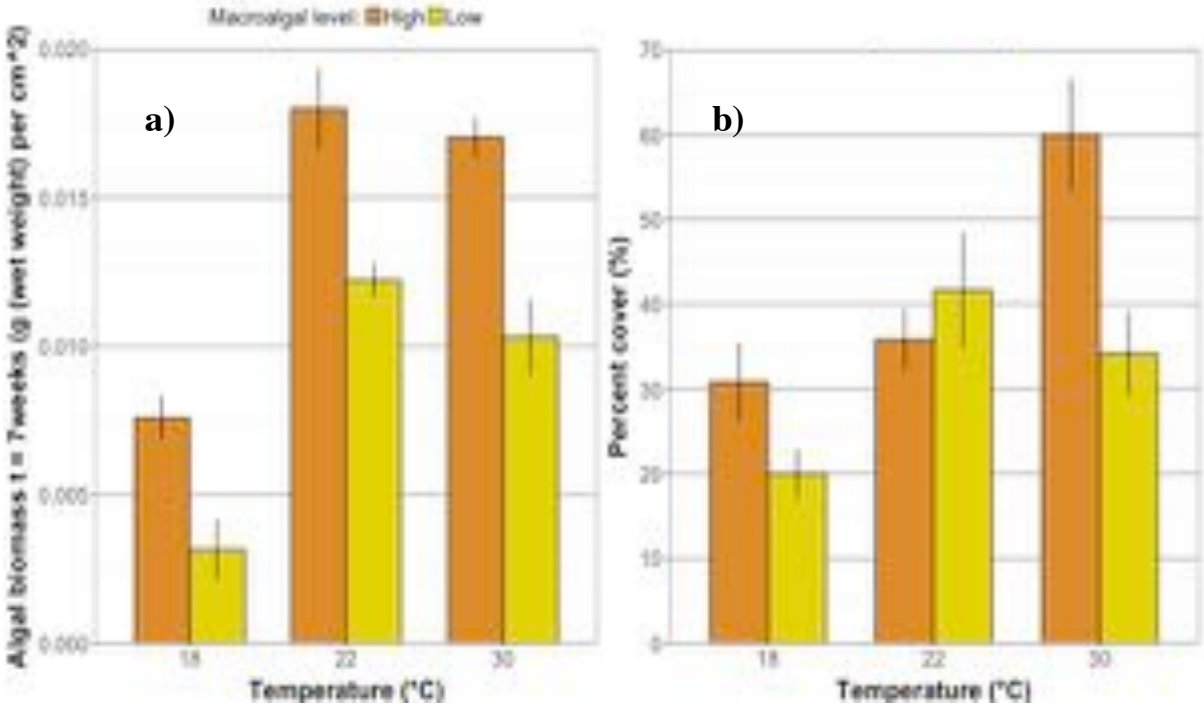

Figure 13: *Gracilaria gracilis* a) biomass and b) percent cover at the end of the 7-week experiment across three temperature treatments and two *Gracilaria* additions. Columns represent mean values ± 1 SE, n = 3. Note that all values in the control groups are equal to 0 and were therefore not included.

Table 12: Tukey's pairwise comparison of group means in *Gracilaria* biomass and percent cover at the end of the seven-week experiment between temperature treatments and *Gracilaria* additions, as well as between the interaction between temperature and *Gracilaria* levels, for the percent cover. Significant results ($p < 0.05$) are highlighted in **bold**.

Groups	Mean difference	P
	a) *Gracilaria* biomass	
18 – 22	-0.0097	**< 0.001**
18 – 30	-0.0083	**< 0.001**
22 – 30	0.0014	0.348
L – H *	-0.0057	$\mathbf{1.430 \times 10^{-5}}$
	b) *Gracilaria* percent cover	
18 – 22	-13.333	0.0573
18 – 30	-21.667	**0.003**
22 – 30	-8.333	0.276
L – H*	-10.28	**0.031**
18H – 18L	10.833	0.678
18H – 22H	-5.000	0.980
18H – 22L	-10.833	0.678
18H – 30H	-29.167	**0.017**
18H – 30L	-3.333	0.997
18L – 22H	-15.833	0.315
18L – 22L	-21.667	0.094
18L – 30H	-40.000	**0.002**
18L – 30L	-14.167	0.423
22H – 22L	-5.833	0.962
22H – 30H	-24.167	0.053
22H – 30L	1.667	1
22L – 30H	-18.333	0.193
22L – 30L	7.500	0.899
30H – 30L	25.833	**0.036**

* Note that comparisons with the Control group was not done as all values in that group are equal to 0

Gracilaria fouling

Only temperature had a statistically significant effect on fouling of *G. gracilis* by microalgae ($F_{2,12} = 138.451; p = 5.140 \times 10^{-9}$; Table 13). Fouling was lowest at 18℃

(mean score = 1.6 ± 0.1 out of 5 compared to 4.0 ± 0.1 at 30℃) but increased with rising temperature and all temperature treatments were statistically different from one another ($p_{18-22} = 0.003, p_{18-30} < 0.001$ and $p_{22-30} < 0.001$; Table 14; Fig. 14). The additions of macroalga ($F_{1,12} = 0.074; p = 0.791$) and the interaction between temperature and *Gracilaria* ($F_{2,12} = 0.959; p = 0.411$) did not affect the fouling of *G. gracilis* (Table 13).

Table 13: Two-way ANOVA results assessing the individual and interactive effects of temperature and macroalgal levels on the fouling of *Gracilaria*. Significant results (p < 0.05) are highlighted in **bold**. Levene's test: p = $F_{5,12} = 0.249; p = 0.933$.

Source of variation	Df	SS	F	p
Temperature	2	18.768	138.451	$\mathbf{5.140 \times 10^{-9}}$
Gracilaria levels	1	0.005	0.074	0.791
Temperature × *Gracilaria*	2	0.130	0.959	0.411
Residuals	12	0.813		

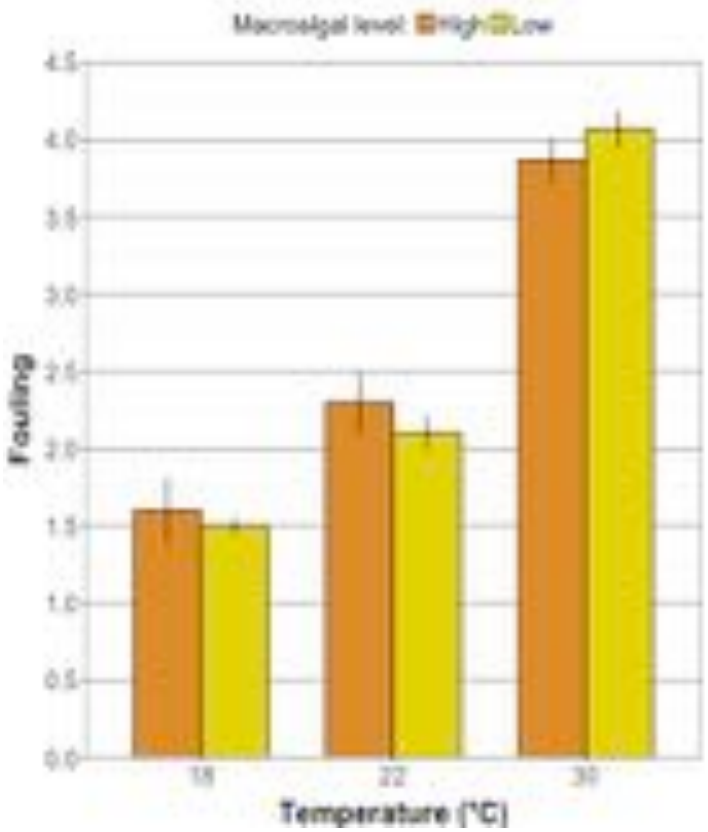

Figure 14: *Gracilaria gracilis* fouling at the end of the 7-week experiment across three temperature treatments and two *Gracilaria* additions. Fouling was determined based on a scale ranging from 1 (not fouled) to 5 (heavily fouled). Columns represent mean values ± 1 SE, n = 3. Note that all values in the control groups are equal to 0 and were therefore not included.

Table 14: Tukey's pairwise comparison of group means in *Gracilaria* fouling between temperature treatments. Significant results ($p < 0.05$) are highlighted in **bold**.

Groups	Mean difference	P
18 – 22	-0.650	**0.003**
18 – 30	-2.417	**< 0.001**
22 – 30	-1.767	**< 0.001**

Discussion

This study revealed that while cover of the macroalga *Gracilaria gracilis* over a seven-week period did not significantly affect the overall performance of *Zostera capensis*,

increasing temperature had significant idiosyncratic effects on both the seagrass and the macroalga.

Widespread declines in seagrass distribution have been largely attributed to colonisation by epiphytes, which impair internal physiology and ultimately damage seagrass leaves (Burnell et al., 2014; Cowper, 1978; Sand-Jensen & Borum, 1983). Drift algae and epiphytes are intrinsic components of seagrass beds and largely contribute to seagrass dynamics (da Silva & Asmus, 2001). Indeed, epiphyte production can approximate as much as 20% of seagrass production (van Montfrans et al., 1984) and can contribute a significant proportion of total producer biomass (Talbot & Bate, 1987). The growth of epiphytic autotrophs is stimulated by temperature and by intercepting light as a result of their physical position in the water column (Burnell et al., 2014; Larkum et al., 2009; Lepoint et al., 1999). This ultimately shades seagrasses thus reducing growth rates, photosynthesis and hence diffusion rates of carbon and oxygen across seagrass leaves, exerting a 'bottom-up' control (Anderson et al., 1996; Biber et al., 2004; Höffle et al., 2011; Hughes et al., 2004; Huo et al., 2012; Sand-Jensen & Borum, 1983). This attenuation of light by epiphytes detrimentally affect most seagrasses, leading some to suggest that the latter may lead to localised seagrass losses (van Montfrans et al., 1984). Our findings indicate greater seagrass fouling at 30℃, while low levels were recorded at the two lowest temperatures. Heavy fouling at 30℃ was also accompanied by a greater biomass of senescent leaves. These results support prior research demonstrating a proliferation of epiphytic material with increasing temperature, which would likely deteriorate the condition of the seagrass leaves.

Samples at 30℃ did not only experience higher levels of fouling and senescent biomass, but also greater leaf width and a marginally greater leaf surface area. This finding was particularly counterintuitive at first since there is ample evidence of *Z. capensis*

developing shorter, narrower leaves in response to environmental stress such as exposure, desiccation and damage from wave action for instance (Adams, 2016; Talbot & Bate, 1987). Personal observations from Langebaan Lagoon also suggest that increased environmental stress resulted in shorter and thinner leaves. More specifically, seagrass leaves are narrower and shorter at Geelbek, which is located in the southern end of the lagoon. In this region, species, including seagrasses, have to endure higher temperatures, which can reach a maximum of 30℃ in summer, increased salinities, which can rise up to 38‰ due to evaporation and greater aerial exposure (Christie & Moldan, 1977; Shannon & Stander, 1977). Consequently, reduced leaf surface area might be an adaptation to protect against varying and extreme environmental conditions.

Additionally, there is widespread evidence indicating that seagrasses can develop two major forms: a narrow and a wide form, and that the development of wider leaves is a response to decreased light availability (Den Hartog, 1970; Hedge et al., 2009; Johnstone, 1978; McMillan, 1983; Peralta et al., 2000; Sidik et al., 1999; York et al., 2013). Seagrasses are adapted to high-light environments (Fong & Harwell, 1994) and require more than 10% of the surface irradiance to survive (Duarte, 1991; Vaudrey, 2008). Macroalgae on the other hand, can thrive under light ranging from 0.12 to < 0.003% of surface irradiance, for both thicker and thinner species (Markager & Sand-Jensen, 1992), although exceptionally low maintenance respiratory requirements are required for growth in environments with less than 1% of surface irradiance available (Sand-Jensen, 1988). Therefore, by promoting the growth of wider leaves under high light stress, seagrass plants effectively increase above-ground biomass in order to obtain the same photosynthetic output as a narrow leaf (Hedge et al., 2009; Peralta et al., 2005; Voronin et al., 2003).

In a similar vein, while univariate statistics did not indicate any statistical differences in means, multivariate statistics did suggest lower below-ground biomass at highly elevated

temperature. It was also highlighted earlier that seagrass leaves were significantly more fouled at 30℃ thus reducing light availability necessary for photosynthesis. In environments where light is a limiting factor, oxygen consumption by roots can detrimentally impact the carbon balance of seagrass and thereby reduce vitality and survival potential (Hemminga, 1998). Carbon starvation may therefore become problematic for below-ground components as the decline in photosynthetic activity can result in hypoxic or anoxic conditions (Hemminga, 1998). However, studies suggest that seagrass plants can either downregulate or upregulate below-ground biomass (compared to the above-ground biomass) in response to diverse environmental factors (Ferguson et al., 2016; Lee & Dunton, 2000; Schanz & Asmus, 2003). Seagrass species might also alter their above-ground to below-ground biomass ratio in an attempt to stabilise respiratory demands and photosynthetic production (Dennison, 1987; Ferguson et al., 2016; Hemminga & Duarte, 2000). Therefore, as a result of declining photosynthetic activity caused by heavy fouling at 30℃, one could speculate that in addition to increasing above-ground biomass, *Z. capensis* compensates by decreasing its below-ground material, in an attempt to reduce oxygen consumption by the roots.

In contrast to *Z. capensis*, *G. gracilis* generally appeared to perform better at higher temperatures, with increased biomass and percent cover observed in spite of high epiphyte loads. Fouling is often considered as an important problem in the cultivation of *Gracilaria* (Fletcher, 1996). It must be noted that the biomass measures of *G. gracilis* also include the epiphyte biomass and that the biomass of *Gracilaria* therefore represents overestimates, especially under the two highest temperatures, with 22℃ being affected to a lesser extent. Nonetheless, the general trend is that the macroalga performed better at 22℃ and 30℃, with mean biomass values being close to the original weight and depreciating greatly at 18℃. This enhanced biomass at higher temperatures was expected, as a number of studies have

demonstrated a positive effect of temperature on the growth of *Gracilaria gracilis* (Engledow & Bolton, 1992; McLachlan & Bird, 1984). Additionally, research has shown that growth rate can increase under higher temperatures, exceeding 10% per day, in contrast to growth halting or being stunted during cooler months (Huo et al., 2012; Huo et al., 2011; Largo et al., 1989). The latter trend was also evident in my experiment.

It was initially theorised that the enhanced growth of *Gracilaria* caused by temperature would have either an additive or synergistic impact on *Z. capensis* (see Introduction p.17) and therefore detrimentally impact seagrass performance by limiting light and carbon available for photosynthesis (Huntington & Boyer, 2008; Moore et al., 1996; Vaudrey, 2008). As its biomass increased, *Gracilaria gracilis* did cover a larger area with increased temperature. The significant interaction between temperature and macroalgal levels is likely due to lower temperature and low levels of macroalga inducing smaller percentage cover than higher temperatures. However, it is highly likely that macroalgal biomass would first need to reach a certain threshold value before negatively impacting seagrass performance and triggering any transitions between from a seagrass- to macroalgal-dominated state (Huntington & Boyer, 2008). For example, Huntington and Boyer (2008) and Holmer et al. (2011) reported highly significant effects of macroalgae on their seagrass species (*Halophila ovalis* and *Zostera marina*) with high macroalgal density reducing the surface irradiance reaching the substrate to only 2% (Huntington & Boyer, 2008), resulting in declining seagrass shoot density. The authors tested the effects of 1700 g (wet weight).m^{-2} and 3400 g (wet weight).m^{-2} of *Gracilariopsis andersonii* and *Gracilaria comosa,* respectively, on seagrasses. In comparison, I used a maximum of approximately 173.3 g (wet weight).m^{-2} of *G. gracilis*, potentially suggesting that additions of macroalga in this study were not high enough to sufficiently shade seagrass leaves and cause any deleterious effects.

It is also possible that my experiment was not run long enough for *G. gracilis* cover to detrimentally impact seagrass performance.

From the results obtained, it appears that beds of *Zostera capensis* in Langebaan Lagoon will likely decline in response to rising sea surface temperatures, whereas co-occurring *Gracilaria gracilis* will not be as substantially impacted, with some traits responding positively. This notion is in agreement with previous studies, which have reported a higher optimum temperature for *G. gracilis*, estimated at 25℃ (Engledow & Bolton, 1992), compared to 15-20℃ for *Z. capensis* (Edgecumbe, 1979; Short et al., 2010). Rising temperature will likely stimulate the proliferation of macroalgae and epiphytic material (which typically exhibit faster growth rates), thereby increasing competition for resources and light between these autotrophs (Fong & Harwell, 1994; Sidik et al., 2001; Zaldívar et al., 2009). For plant engineers, competition could lead to the displacement of one species at the expense of another, which will have significant consequences for organisms dependent on the resources modulated by engineers (Jones et al., 1997). As commented by Jones et al. (1994, p. 378), 'it is obvious, but surprisingly rarely explicitly stated, that numerous inhabitants of the habitats so created are dependent upon the physical conditions modulated by the autogenic engineers, and upon resource flows which they influence but do not directly provide; without the engineers, most of these organisms would disappear'.

Changes in the structure, abundance and distribution of seagrass ecosystems could therefore have massive repercussions for both regional and local biota (Short & Neckles, 1999). Although the Cape eelgrass can be found from Langebaan Lagoon to Kenya (Supp. Fig. 1-2), its distribution is markedly fragmented and patchy (Adams, 2016; Short et al., 2010). At the population-level, such fragmentation could result in lowered dispersal potential, thereby impairing recolonisation by extant subpopulations and precipitating the collapse of the metapopulation, as illustrated by the sudden disappearance of Allegheny woodrats in

New York in the 1970s (LoGiudice, 2006). In Langebaan Lagoon, large-scale losses of *Zostera capensis* cover between 1983 and 2009 have led to a decrease of 20 to 50% in invertebrate richness and a decline of 20 to 70% in invertebrate abundance (Pillay et al., 2010). More importantly, the critically endangered and endemic limpet, *Siphonaria compressa*, is more particularly at risk of extinction since the species is known to occur in only two locations in South Africa and feeds exclusively on the blades of *Z. capensis* (Angel et al., 2006; Herbert, 1999). As such, it becomes vital to maintain biodiversity, structure and integrity of this ecosystem in order to prevent it from deteriorating into undesired states (Folke et al., 2004).

In some ways, seagrasses and macroalgae provide a superficially analogous structural and functional role in ecosystems (Mineur et al., 2015). Indeed, they both provide a physical structure which acts as a shelter for epibiota (Coleman & Williams, 2002; Schmitt & Holbrook, 1990; Zieman, 1982), entrain larvae (Coleman & Williams, 2002), modify the near-bottom hydrodynamic flow regimes underneath the canopies (Fonseca et al., 1982; Hansen & Reidenbach, 2013; Jackson & Winant, 1983), and change the behaviour and effectiveness of predators (Coen et al., 1981; Leber, 1985; Main, 1987). Consequently, in the event of a shift from seagrass- to macroalgal-dominated state, some ecosystem functions provided by *Z. capensis* might not be entirely lost but might however lead to a change in species assemblages.

Lastly, global warming represents only one dimension of human-induced climate change and occurs simultaneously with numerous other types of stressors, which all interact (Koch & Mooney, 1995; Shaver et al., 2000; Vitousek et al., 1997). We do not know whether the impacts of temperature observed in this experimental study would be strengthened or weakened by fluctuations in other stressors or the combined effects of those. Perhaps the

combination of those factors will accelerate or decelerate change relative to individual effects (Walther et al., 2002). For instance, Hoffman et al. (2003) suggested an interaction between temperature and UV radiation in regulating survival of autotrophic propagules, with survival occurring at all levels of UV in warm water but high mortality at high levels of UV in cooler water. Similarly, Reynaud et al. (2003) reported that while coral calcification rates were not affected by an increase in partial pressure of CO_2 at 25℃, rates were reduced by 50% at 28℃ thus demonstrating an interaction between temperature and pCO_2.

In Langebaan Lagoon, temperatures are closely linked to nutrient concentrations, with oligotrophic (almost 0 $\mu M.N$ after December) conditions associated with winter, and nutrient-rich (5-200 $\mu M.N$) conditions observed during summer (Anderson et al., 1996). This provides an additional competitive advantage to macroalgae, which typically thrive under high nutrient concentrations in the water column (Holmer et al., 2003; Zaldívar et al., 2003), as opposed to seagrasses, for which sediment composition is of greater importance (Adey & Loveland, 2011; Short, 1987). This is also shown by the distribution of *G. gracilis* along the west coast of Africa, where chlorophyll *a* concentrations are higher on average than on the east coast (Supp. Fig. 2). It is predicted that atmospheric pressure gradients, and therefore wind fields, will intensify along ocean margins due to the warmer conditions over continental interiors, as opposed to oceans. Greater wind fields could lead to more upwelling in eastern boundary currents and so increase nutrient availability at the sea surface (Bakun, 1990; Bakun et al., 2015; Enayatmehr & Azad, 2013). This notion is supported by paleoclimatic data suggesting a positive correlation between temperature (over millennial timescales) and upwelling in the California current system, with documented increases in upwelling events along the coast of California over the past 30 years (Pisias et al., 2001; Snyder et al., 2003). Increased sea surface temperature could also result in a stronger thermal stratification and a deepening of the thermocline, which could then inhibit the upwelling of cool, nutrient-rich

waters (Roemmich & McGowan, 1995). In the case of the Benguela Upwelling System, although some studies project an intensification of upwelling winds (García-Reyes et al., 2015; Wang et al., 2015), others did not support the latter (Tim et al., 2015), rendering predictions more controversial. Even so, seagrasses are only able to outcompete macroalgae when nutrients are found in low concentrations due to their ability to draw nutrients from the sediments while macroalgae dominate when light is the only limiting factor and under high nutrient concentrations (Holmer et al., 2003; Scheffer et al., 2003; Zaldívar et al., 2003). This finding is supported by the fact that *Z. capensis* occurs along the eastern side of Africa, where chlorophyll *a* concentrations seem lower, but not on the western coast (Supp. Fig. 2).

Conclusions

Overall, there was no interactive effect of the two stressors chosen in this study and temperature had a substantial negative impact on *Z. capensis,* with highly elevated temperatures (30℃) having a much greater impact than control (18℃) and elevated (22℃) temperatures. Additionally, the study showed evidence of morphological plasticity developed by *Z. capensis* with an increase in leaf width and area, to an extent, and a slight decrease in below-ground biomass, in an attempt to maintain carbon balance despite light attenuation caused by heavy fouling and increased respiratory demands in response to increased temperature (Duarte, 2002; Hemminga, 1998; Short & Neckles, 1999). All these variables as well as fouling and senescent biomass were all negatively affected, particularly at 30℃. Conversely, the additions of macroalga did not have any effects on the performance of *Z. capensis*, which might have been due to macroalgal levels being too low. Finally, I conclude that the study was conducted on a too short a timescale to determine whether *Z. capensis* population in Langebaan Lagoon will develop the same characteristics as the one in Kenya, which is able to withstand highly elevated temperatures. However, one is able to predict a

decline in seagrass abundance in response to warming and conversely, a proliferation of macroalga *G. gracilis*. This therefore suggests that a seagrass- to macroalgal-dominated shift might occur in Langebaan Lagoon if temperatures rise.

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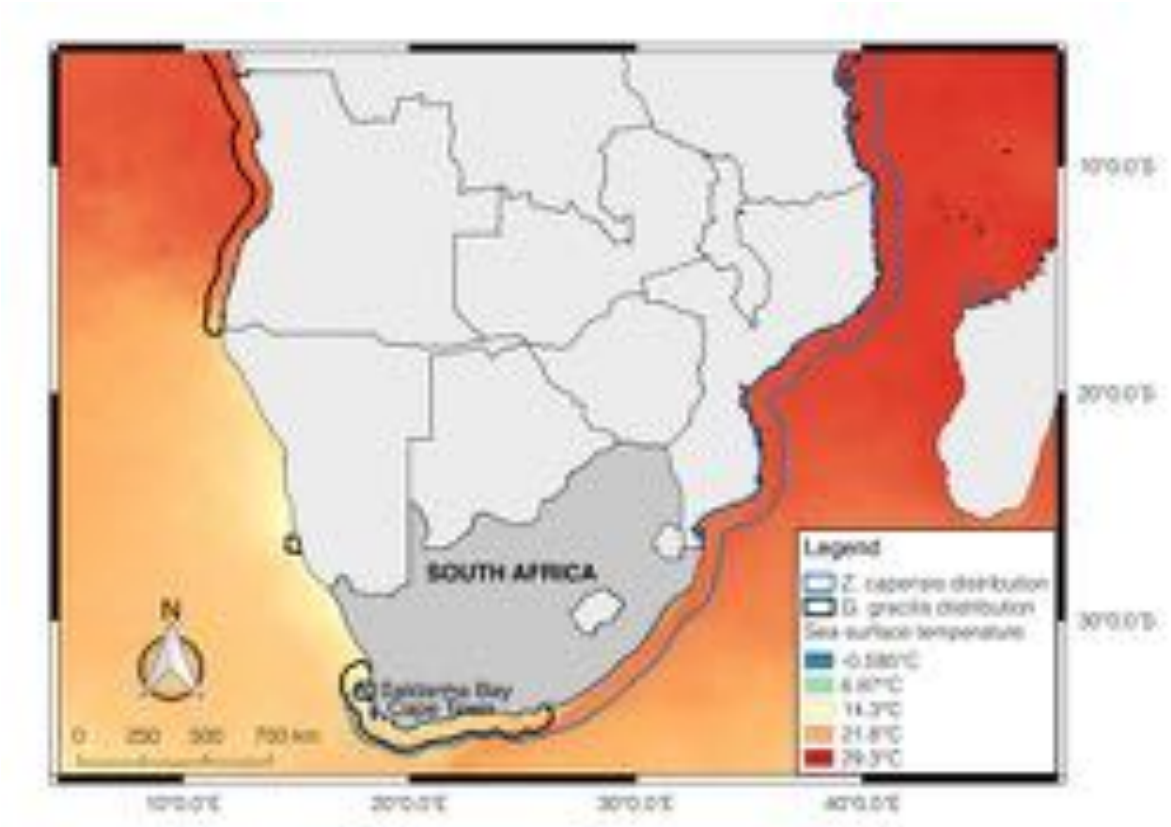
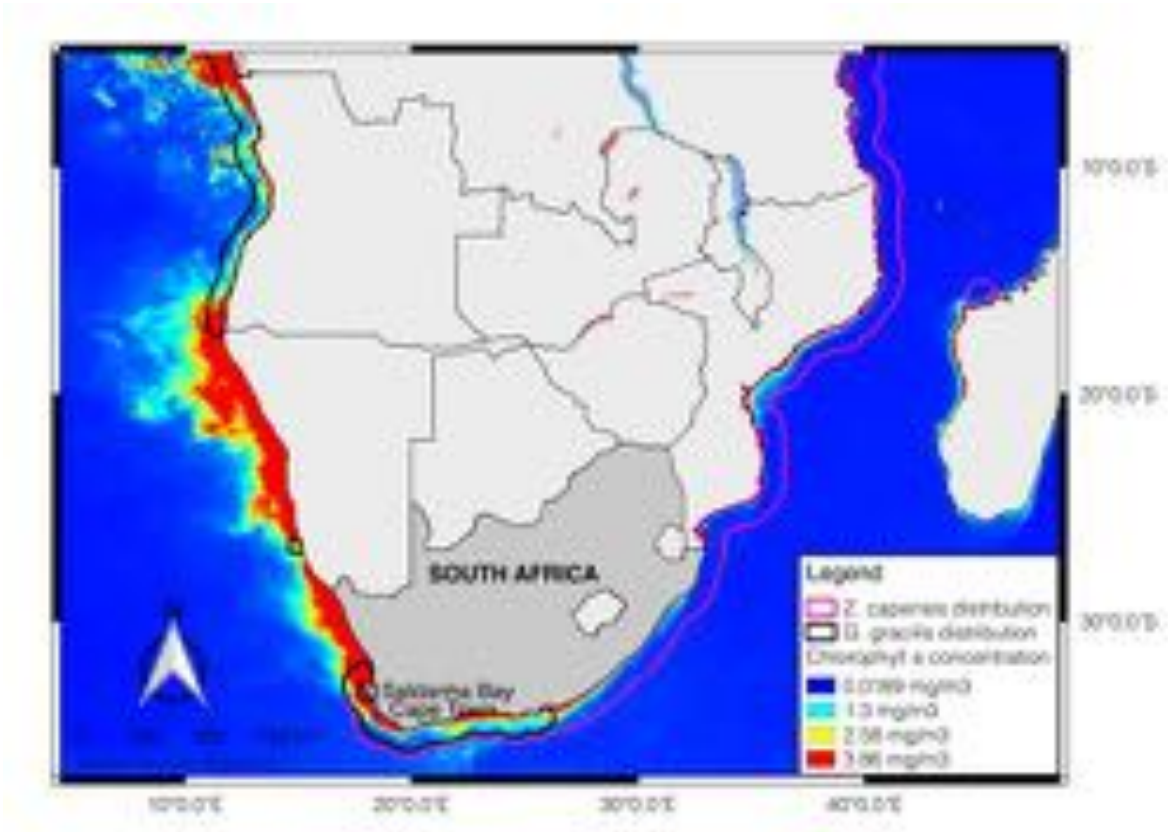
Supplementary Material



Supplementary Figure 1: Distribution map of *Zostera capensis* and *Gracilaria gracilis* in southern Africa and average sea surface temperature (Iyer et al., 2004; Iyer et al., 2005; John et al., 2004; Ocean Biology Processing Group, 2014; Price et al., 1988; QGIS Development Team, 2017; Short et al., 2010).



Supplementary Figure 2: Distribution map of *Zostera capensis* and *Gracilaria gracilis* in southern Africa and average chlorophyll *a* concentrations (Iyer et al., 2004; Iyer et al., 2005; John et al., 2004; Ocean Biology Processing Group, 2014; Price et al., 1988; QGIS Development Team, 2017; Short et al., 2010).

Supplementary Table 1: Mean (± SE) values of all *Zostera capensis* and *Gracilaria gracilis* variables. For macroalgal levels, High = high macroalgal biomass (2.3 g), Low = low macroalgal biomass (1.2 g), and Control = no macroalga added.

Temperature / Macroalgal level	18℃	22℃	30℃
Seagrass density (shoots per pot)			
High	6.67 (2.03)	6.67 (3.94)	8.00 (2.02)
Low	5.50 (3.75)	5.33 (1.76)	8.50 (0.76)
Control	9.50 (4.25)	3.67 (1.64)	11.83 (3.81)
Seagrass leaf length (cm)			
High	9.99 (0.69)	10.52 (0.38)	9.35 (0.42)
Low	9.05 (2.25)	8.84 (1.41)	8.78 (1.07)
Control	11.76 (1.33)	10.30 (1.11)	9.65 (0.66)
Seagrass leaf width (cm)			
High	0.11 (0.01)	0.13 (0.01)	0.19 (0.03)
Low	0.12 (0.01)	0.12 (0.01)	0.18 (0.02)
Control	0.13 (0.00)	0.13 (0.00)	0.18 (0.02)
Seagrass leaf area (cm^2)			
High	1.1510 (0.1586)	1.4305 (0.0959)	1.7395 (0.1768)
Low	1.1614 (0.3733)	1.1223 (0.1711)	1.5627 (0.2678)
Control	1.5366 (0.2347)	1.3827 (0.1819)	1.7201 (0.0551)
Seagrass fouling (cube root transformed) (g of epiphyte per cm^2)			
High	0.1161 (0.0051)	0.1014 (0.0074)	0.1681 (0.0081)
Low	0.1284 (0.0196)	0.1315 (0.0378)	0.1851 (0.0257)
Control	0.0994 (0.0047)	0.0977 (0.0134)	0.1606 (0.0086)
Seagrass senescent biomass (cube root transformed) (g (dry weight) per cm^2)			
High	0.0654 (0.0167)	0.0666 (0.0131)	0.1630 (0.0247)
Low	0.0638 (0.0328)	0.0825 (0.0124)	0.1462 (0.0051)
Control	0.0642 (0.0163)	0.0916 (0.0103)	0.1730 (0.0212)
Seagrass non-senescent biomass (g (dry weight) per cm^2)			
High	6.47×10^{-4} (0.00029)	5.62×10^{-4} (0.00003)	6.45×10^{-4} (0.00018)
Low	5.42×10^{-4} (0.00023)	7.03×10^{-4} (0.00014)	8.22×10^{-4} (0.00028)
Control	7.03×10^{-4} (0.00057)	4.24×10^{-4} (0.00019)	4.42×10^{-4} (0.00007)
Seagrass below-ground biomass (cube root transformed) (g (dry weight) per cm^2)			
High	0.1817 (0.0067)	0.1813 (0.0180)	0.1872 (0.0147)
Low	0.1749 (0.0031)	0.1655 (0.0088)	0.1904 (0.0259)
Control	1.1974 (0.0060)	0.1721 (0.0082)	0.1923 (0.0103)

Temperature / Macroalgal level	18℃	22℃	30℃
***Gracilaria* biomass (g (wet weight) per cm^2)**			
High	7.5860×10^{-3} (0.0007)	1.7998×10^{-2} (0.0014)	1.7044×10^{-2} (0.0007)
Low	3.1525×10^{-3} (0.0010)	1.2221×10^{-2} (0.0006)	1.0312×10^{-2} (0.0013)
Control	0	0	0
***Gracilaria* percent cover (%)**			
High	30.83 (4.64)	35.83 (3.63)	60.00 (6.61)
Low	20.00 (2.89)	41.67 (6.82)	34.17 (5.07)
Control	0	0	0
***Gracilaria* fouling**			
High	1.6 (0.2)	2.3 (0.2)	3.9 (0.1)
Low	1.5 (0.1)	2.1 (0.1)	4.1 (0.1)
Control	0	0	0